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# Sperm Ultrastructure in the Cirripedia and its Phylogenetic Significance

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ABSTRACT. Sperm morphology was examined in 42 species of Thoracica, from 32 genera in 11 families, and in one species of Acrothoracica. The filiform spermatozoa of Thoracica, Acrothoracica and Rhizocephala share: (1) an axoneme capped by a conical acrosome; (2) a filiform nucleus running parallel to the axoneme; (3) an elongate mitochondrion posterior to the nucleus; (4) glycogen deposits. This sperm type links the Thoracica, Acrothoracica and Rhizocephala and distinguishes them from the other Thecostraca. Structural differences in the sperm nucleus separate the three groups and are further consistent with segregation of the Rhizocephala from the Thoracica + Acrothoracica (= Cirripedia *sensu* Newman). In spermatozoa from seminal vesicles of Thoracica, an accessory droplet is usually present. This structure, produced by the Golgi complex during spermiogenesis, shows variation among species in its form and internal substructure. The Iblidae, Lepadidae and Scalpellidae have distinctive modifications of the accessory droplet. Among the scalpellids, the Pollicipedinae retain a generalised thoracican sperm morphology, while other subfamilies which have been studied (Lithotryinae, Scalpellinae, Calanticinae) display differing modifications of nuclear and droplet structure. Sperm morphology of *Verruca* is consistent with derivation of the Verrucomorpha from scalpelloids related more closely to the Pollicipedinae than to the Calanticinae, Lithotryinae or Scalpellinae. The retention of a generalised sperm morphology in *Catomerus* is further consistent with the derivation, on other grounds, of the Balanomorpha from a scalpelloid ancestry. Within the Balanomorpha, sperm data offer indications of phylogenetic patterns in the Chthamaloidea (*Chamaesipho* derived from catophragmids independently of the chthamalids), Coronuloidea (*Cylindrolepas* related to *Tubicinella*; tetraclitids monophyletic and including *Austrobalanus*) and Balanoidea (archaeobalanids polyphyletic; *Armatobalanus* related to Pyrgomatidae; *Balanus* and the megabalanines both probably complex groups of perhaps multiple origins). Present sperm data do not assist in the elucidation of relationships between balanomorph superfamilies. Basal members of each superfamily retain a generalised thoracican sperm structure.

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Among the Crustacea, only the maxillopod groups Thecostraca (*sensu* Grygier, 1987a; Newman, 1987), Branchiura and Mystacocarida retain an axoneme in their spermatozoa (Brown & Metz, 1967; Brown, 1970; Munn & Barnes, 1970a, 1970b; Wingstrand, 1972, 1978, 1988; Pochon-Masson, 1978; Kubo *et al.*, 1979; Grygier, 1981, 1982, 1987a). In other crustaceans, sperm motility is either wanting, (e.g. Decapoda) or achieved using other structures (e.g. Ostracoda, Baccetti & Afzelius, 1976; Pochon-Masson, 1978; Wingstrand, 1988). Grygier (1981, 1982, 1987a) showed that spermatozoa of the Ascothoracida (Fig. 1a,b) are readily discernible ultrastructurally from those of the Thoracica, Acrothoracica and Rhizocephala and suggested that the Ascothoracida should be separated from the Cirripedia as then defined, probably as a category of equal rank. A more complex interpretation of the higher classification of the bivalved maxillopodans has been proposed by Newman (1987) and Grygier (1987b), in which the Rhizocephala are also classified as a group of equal rank to the Ascothoracida and Cirripedia, all three being defined as subclasses of the maxillopodan class Thecostraca, which also includes the so-called Y-larvae or Facetotecta. In this classification, the subclass Cirripedia comprises only the Thoracica and Acrothoracica. The Thoracica, Acrothoracica and Rhizocephala, however, share similar larval stages and a common filiform spermatozoon (Fig. 1c–g), the basic features of which include a conical acrosome at the apex of the axoneme, a filamentous nucleus parallel to the axoneme, a single elongate mitochondrion and glycogen deposit parallel to the axoneme (Munn & Barnes, 1970a, 1970b; Pochon-Masson, 1971). The spermatozoa of thoracicans, acrothoracicans and possibly rhizocephalans also possess an accessory droplet, a basically fusiform body produced by the Golgi complex during the later stages of spermiogenesis (Kubo *et al.*, 1979; Azevedo & Corral, 1982), but then lost in the seminal vesicles, in the anterior portion of the ejaculatory duct, or soon after leaving the penis (Munn & Barnes, 1970b; Barnes *et al.*, 1971; Barnes *et al.*, 1977; Kubo *et al.*, 1979). The accessory droplet is unique to this sperm type and adds further weight to the concept that the filiform sperm of Thoracica, Acrothoracica and Rhizocephala is a synapomorphy, placing the Rhizocephala close to, if not within, the Cirripedia.

Beyond these arguments, the utilisation of sperm ultrastructure in the analysis of cirripede phylogeny has been restricted by lack of data and by the seemingly invariant ultrastructure of the sperm. Ultrastructural data are particularly limited in groups such as the Rhizocephala (*Sacculina carcini* — Pochon-Masson, 1971) and Lepadomorpha (*Pollicipes pollicipes* — Azevedo & Corral, 1982; *Lepas anatifera* — Anderson & Personne, 1970). A review of spermatozoa and spermiogenesis in the Rhizocephala is currently being prepared by Hoeg & Jespersen (J. Hoeg, personal communication). The accessory droplet of balanomorph spermatozoa is known to vary in internal structure from species to species (for example Munn & Barnes, 1970b; Kubo *et al.*, 1979), but no attempt has been made to relate this structure to phylogeny. In the present work, we offer comparative data on sperm ultrastructure in a wide range of species, with particular emphasis on specific variation in the ultrastructure of the accessory droplet. We then review the ultrastructure of thecostracan sperm as presently known and consider the relevance of the accessory droplet as a phylogenetic character.

Abbreviations used in the figures are: a — acrosomal complex; ar — axial rod material (of acrosomal complex); av — acrosomal vesicle; ax — axoneme; c — centriole; co — collar; d — accessory droplet; drs — dense ring structure (annulus); g — glycogen deposits; l — lacunae (substructural element of droplet); m — mitochondrion; n — nucleus; r — rod (substructural element of droplet); t — tail; v — dense vesicle(s) (substructural element of droplet).

## Materials and Methods

Spermatozoa were obtained from the seminal vesicles of one species of acrothoracican and 42 species of thoracican cirripedes. The seminal vesicles were taken either from live specimens or from sea water-formalin fixed material. Table 1 lists the species examined, together with relevant locality data and fixation used. For live specimens, seminal vesicles were dissected out, cut into small portions (1 to 2 $mm^3$) and fixed in cold (0 to 4°C) 3% glutaraldehyde (in 0.2 M phosphate or cacodylate buffer) for two to three hours. Subsequently, the tissues were washed in buffer, as were tissues obtained from formalin-fixed specimens. All tissues, whether glutaraldehyde or formalin-fixed, were placed in a cold 1% osmium tetroxide solution (in 0.2 M phosphate or cacodylate buffer) for 80 minutes. After a thorough buffer rinse, tissues were dehydrated using ethanol and embedded in Spurr's epoxy resin. Ultrathin sections were cut using a LKB ultramicrotome, collected on uncoated copper grids and stained using 4% uranyl acetate and Reynold's lead citrate. Sections were examined using a Philips 300 transmission electron microscope operated at 60kV.

## Results

### Acrothoracica (*Berndtia fossata*)

In *Berndtia fossata*, the filiform sperm (Fig. 2a) is approximately 85 µm long. The acrosome is conical and basally invaginated (Fig. 2b). Axial rod material occupies the invagination. A collar appears to be present but is not well developed. A 9 + 2 axoneme, a filiform nucleus and an accessory droplet run parallel to each other (Fig. 2c,d). Transverse sections of the nucleus reveal a dumb-bell shaped profile, similar to that demonstrated by Tomlinson (1969) and Pochon-Masson (1971) for *Trypetesa* (Fig. 2c). This shape may be characteristic for Acrothoracica. The accessory droplet in *Berndtia* is very narrow and exhibits prominent sub-spherical spaces (Fig. 2d). Parallel layers, each composed of a double membrane, occur within the

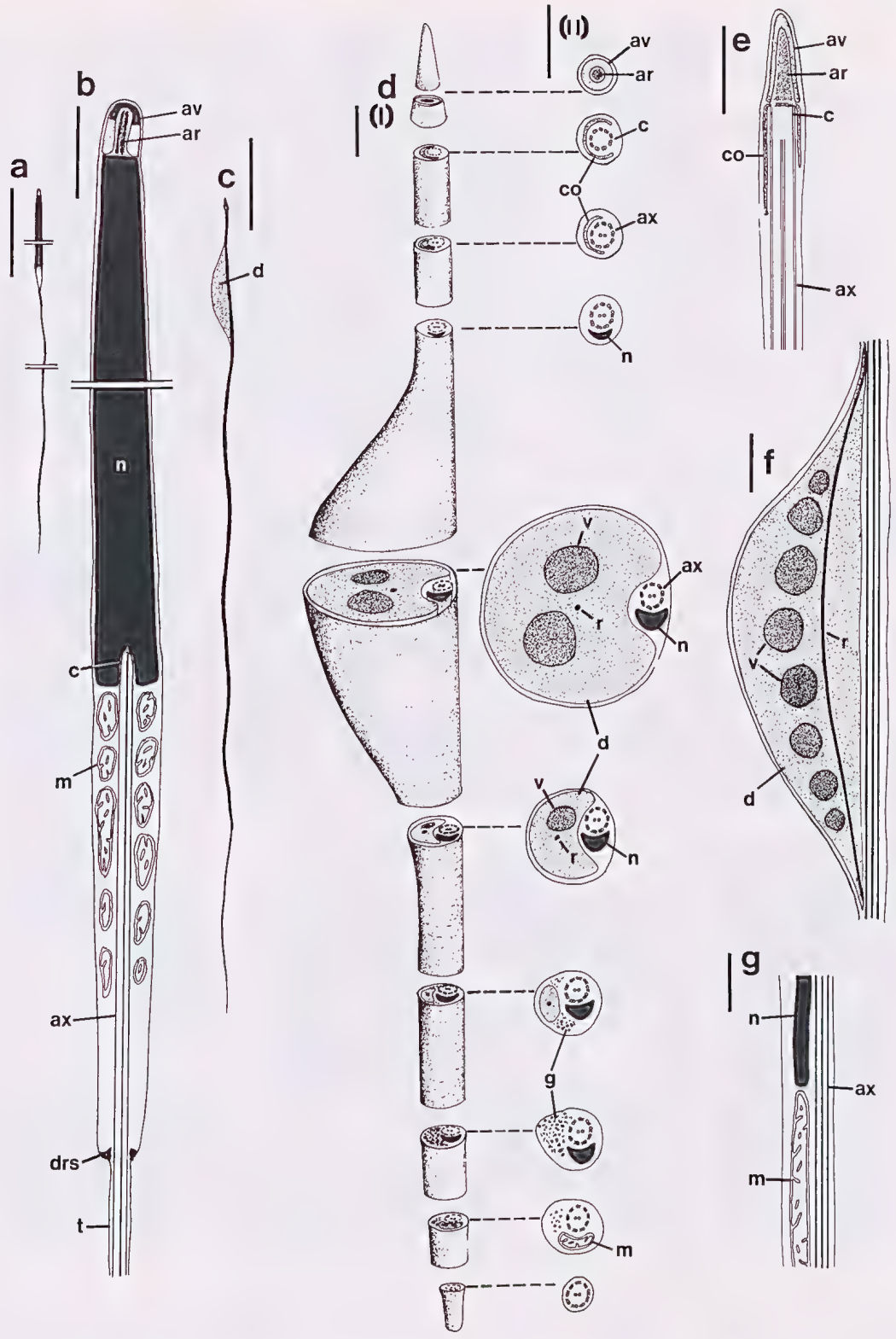


**Fig.1.** Sperm morphology in the Ascothoracica and Cirripedia (semi-diagrammatic). (a, b) Spermatozoon of the ascothoracican, *Ulophysema oeresundense* Brattström (based on data of Grygier, 1982). (c — g) General features of spermatozoa of the Acrothoracica, Thoracica and Rhizocephala. Elongate nucleus (n) runs parallel to axoneme (ax); centriole (c) is adjacent to base of acrosome; single mitochondrion (m) lies posterior to nucleus; accessory droplet (d) (often with internal rod (r) or dense vesicles (v), parallels axoneme/nucleus. (c) Whole spermatozoon. (dI, II) Reconstruction of main sperm regions (example *Austromegabalanus nigrescens*). (e) Longitudinal section of acrosome, centriole and collar. (f) Longitudinal section of droplet and axoneme. (g) Junction between nucleus and mitochondrion. Scale bars: a,c = 10 μm; b = 1.0 μm; all others = 0.5 μm

Table 1. Material examined.

| Species | Locality | Fixation |
|---|---|---|
| ORDER ACROTHORACICA | | |
| *Berndtia fossata* Tomlinson | Darwin, NT | SWF |
| ORDER THORACICA | | |
| Suborder LEPADOMORPHA | | |
| Superfamily Ibloidea | | |
| Family Iblidae | | |
| *Ibla quadrivalvis* (Cuvier) | Balmoral, Sydney, NSW | Glut. |
| Superfamily Scalpelloidea | | |
| Family Scalpellidae | | |
| *Scalpellum stearnsi* Pilsbry | | SWF |
| *Scalpellum* sp. | | Os. |
| Subfamily Lithotryinae | | |
| *Lithotrya valentiana* (Gray) | Lizard Island, northern QLD | SWF |
| Subfamily Calanticinae | | |
| *Calantica spinosa* (Quoy & Gaimard) | Werrington, Otago, NZ | SWF |
| *Calantica villosa* (Leach) | Werrington, Otago, NZ | SWF—>ETH |
| *Smilium peronii* (Gray) | Perth, WA | SWF |
| Superfamily Lepadoidea | | |
| Family Lepadidae | | |
| *Lepas anserifera* Linnaeus | Port Hacking, NSW | |
| *Lepas anatifera* Linnaeus | Port Hacking, NSW | Glut. |
| *Lepas pectinata* Spengler | Port Hacking, NSW | SWF |
| *Conchoderma auritum* (Linnaeus) | Port Hacking, NSW | SWF |
| *Conchoderma virgatum* (Spengler) | Port Hacking, NSW | Glut. |
| Suborder VERRUCOMORPHA | | |
| Family Verrucidae | | |
| *Verruca ströemia* (O.F. Müller) | Plymouth, UK | SWF—>ETH |
| SuborderBALANOMORPHA | | |
| SuperfamilyChthamaloidea | | |
| Family Catophragmidae | | |
| *Catomerus polymerus* (Darwin) | Balmoral, Sydney, NSW | Glut. |
| Family Chthamalidae | | |
| *Chthamalus antennatus* Darwin | Balmoral, Sydney, NSW | Glut. |
| *Chthamalus malayensis* Pilsbry | Townsville, northern QLD | SWF |
| *Octomeris brunnea* Darwin | Magnetic Island, northern QLD | SWF |
| *Chamaesipho tasmanica* Foster & Anderson | Balmoral, Sydney, NSW | Glut. |
| Suborder BALANOMORPHA (cont'd) | | |
| Superfamily Coronuloidea | | |
| Family Coronulidae | | |
| *Coronula diadema* (Linnaeus) | unknown, Australia | SWF |
| *Chelonibia testudinaria* (Linnaeus) | Mon Repos, northern QLD | SWF |
| *Tubicinella cheloniae* Monroe | Mon Repos, northern QLD | SWF |
| *Cylindrolepas darwiniana* Pilsbry | Mon Repos, northern QLD | SWF |
| *Platylepas coriacea* Monroe | Port Jackson, NSW | SWF |
| *Platylepas hexastylos* (Fabricius) | Port Jackson, NSW | SWF |
| Family Tetraclitidae | | |
| *Austrobalanus imperator* (Darwin) | Balmoral, Sydney, NSW | Glut. |
| *Epopella plicata* (Gray) | Werrington, Otago, NZ | SWF |
| *Tetraclita squamosa* (Bruguiere) | Townsville, northern QLD | SWF |
| *Tetraclitella purpurascens* (Wood) | Balmoral, Sydney, NSW | Glut. |
| *Tesseropora rosea* (Krauss) | Balmoral, Sydney, NSW | Glut. |
| Superfamily Balanoidea | | |
| Family Archaeobalanidae | | |
| *Hexaminius foliorum* Anderson, Anderson & Egan | Iron Cove, NSW | Glut. |
| *Hexaminius popeiana* Foster | Iron Cove, NSW | Glut. |
| *Elminius covertus* Foster | Iron Cove, NSW | Glut. |
| *Armatobalanus allium* (Darwin) | Darwin, NT | SWF |
| *Armatobalanus arcuatus* Hoek | Darwin, NT | SWF |
| *Acasta spongites* Poli | | |
| Family Pyrgomatidae | | |
| *Pyrgoma cancellata* Leach | Darwin, NT | SWF |
| *Creusia spinulosa* Leach | John Brewer Reef, Townsville, QLD | SWF |
| *Savignium elongatum* (Hiro) | John Brewer Reef, Townsville, QLD | SWF |
| Family Balanidae | | |
| *Balanus variegatus* Darwin | Iron Cove, NSW | Glut. |
| *Balanus amphitrite* Darwin | Iron Cove, NSW | Glut. |
| *Megabalanus ajax* (Darwin) | One Tree Island, Great Barrier Reef, QLD | SWF |
| *Austromegabalanus nigrescens* (Lamarck) | Balmoral, Sydney, NSW | Glut. |

Abbreviations: ETH (ethanol); Glut. (glutaraldehyde); Os. (osmium tetroxide); SWF (sea water/formalin)

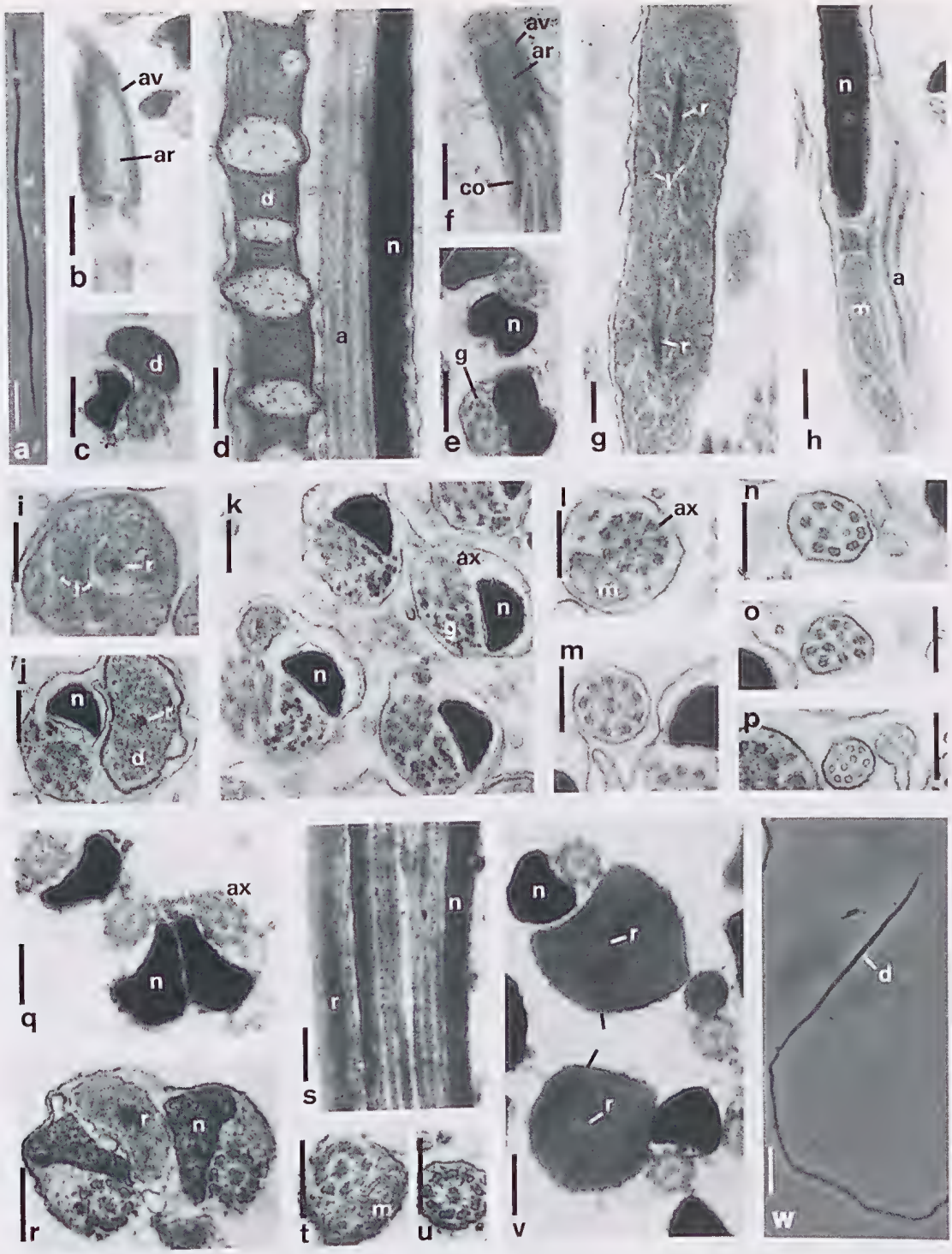


**Fig.2.** (a — e) Spermatozoa of the acrothoracican *Berndtia fossata*. (a) Whole spermatozoon. (b) Longitudinal section through acrosome. (c) Transverse section through nucleus, axoneme and droplet. (d) L.S. through droplet. (e) T.S. nuclei, axonemes, glycogen deposit, droplet. (f — p) *Ibla quadrivalvis* (Thoracica, Iblidae). (f) L.S. acrosome, collar and anterior extremity of axoneme. (g) L.S. portion of droplet showing rod and lacunae. (h) Junction of nucleus and mitochondrion. (i) T.S. rod and lacunae of droplet. (j) T.S. nucleus, axoneme, droplet. (k) T.S. 'glycogen' region of sperm (right) and terminal portion of accessory droplet (left, also with glycogen). (l) T.S. mitochondrial region of sperm. (m) T.S. axoneme of free tail region. (n — p) Sequence of axoneme degeneration at posterior extremity of sperm. (q — w) Scalpellidae. (q) *Scalpellum stearnsi*, T.S. axoneme, nuclei. (r — u) *Scalpellum* sp. (original micrographs courtesy of Professor B.A. Afzelius). (r) T.S. nucleus, droplet (with thick rod) and axoneme. (s) L.S. droplet, nucleus, axoneme. (t) T.S. mitochondrial region of sperm. (u) T.S. free tail. (v, w) *Lithotrya valentiana*. (v) T.S. droplet, nucleus, axoneme. (w) Whole spermatozoon.Scale bars: a,w = 10 μm; b–v = 0.25 μm.

droplet (Fig. 2d). These layers run axially at the periphery of the droplet and transversely at the droplet core (Fig. 2d). The length of the droplet could not be determined. Posterior to the droplet, dense deposits (probably glycogen) occur closely to the nucleus and axoneme (Fig. 2e). A single mitochondrion follows the nucleus in the posterior region of the spermatozoon.

## Thoracica

### Lepadomorpha

### Iblidae — *Ibla quadrivalvis*

The acrosomal vesicle of *I. quadrivalvis* is 0.5 μm long, with a deep basal invagination containing axial rod material (Fig. 2f). Posterior to the acrosomal region is a collar 0.36 μm long, sheathing the centriole and the initial portion of the axoneme (Fig. 2f). Beyond the collar the axoneme becomes closely associated with the filiform nucleus, triangular in transverse section, and an elongate accessory droplet (Fig. 2g,j,k). The droplet measures 14 to 17 μm (phase-contrast observation) and contains a granular matrix, curved spaces (lacunae) and a dense rod 0.04 to 0.91 μm in diameter (Fig. 2g,i,j). Transverse sections indicate that the droplet has a maximum diameter of 0.6 to 0.7 μm (Fig. 2i) and tapers anteriorly and posteriorly (Fig. 2k). Behind the nucleus, the axoneme is accompanied by a single mitochondrion containing unmodified cristae (Fig. 2h). Dense deposits, identifiable as glycogen granules (see Anderson & Personne, 1970 — *Lepas*), form a wedge-shaped tract parallel to the axoneme and nucleus (Fig. 2k) and then to the axoneme and mitochondrion (Fig. 2l). Figures 2m to 2p illustrate degeneration of the 9 + 2 axoneme into individual microtubules at the posterior extremity of the spermatozoon. This involves firstly loss or displacement of the central pair of microtubules, then disruption of doublet positioning (Fig. 2n,o) and finally degeneration of the doublets into single microtubules (Fig. 2p). The spermatozoon of *I. quadrivalvis* is approximately 70 μm long.

### Scalpellidae

Representatives of three scalpellid subfamilies were examined: the Scalpellinae (*Scalpellum stearnsi*, *Scalpellum* sp.), Lithotryinae *(Lithotrya valentiana)* and Calanticinae (*Calantica spinosa*, *Calantica villosa*, *Smilium peronii*). Acrosomes, where observed (*Smilium*, *Calantica*), consist of a conical acrosomal vesicle with a deep basal invagination occupied by axial rod material (Fig. 3b,c). The filiform nucleus and elongate accessory droplet of scalpellid spermatozoa show diversity in morphology. In *Lithotrya*, the nucleus is triangular in transverse section and the droplet is well developed, with a single, pale-staining rod (diameter 0.06 to 0.07 um) at its core (Fig. 2v). In *Scalpellum* the nucleus is also triangular in transverse section, but the profile has a distinct asymmetry (Fig. 2q,r). The accessory droplet of *Scalpellum* sp. is narrow and curved in cross section and contains a thick rod (diameter 0.09 to 0.1 μm) composed of a dense core and outer enveloping layer (see Fig. 2r,s). Droplets were not observed in *Scalpellum stearnsi*. Sperm nuclei of calanticines (*Calantica* spp., *Smilium peronii*) are club-shaped in transverse section (Fig. 3d,f,g,i–l). The accessory droplets of calanticine spermatozoa are long (20 to 27 μm) and up to 0.7 μm wide, with a rod and scattered dense vesicles in *Smilium* (Fig. 3d-g), but without clear evidence of substructure in *Calantica* (Fig. 3k,l). Dense glycogen granules accompany the nucleus and axoneme at and beyond the posterior extremity of the accessory droplet (Fig. 3i). In *Scalpellum*, *Smilium*, and presumably other scalpellids, the nucleus terminates abruptly and is followed by a single mitochondrion (Figs 2t, 3h,j). The mitochondrion usually appears crescentic in transverse section, and is frequently associated with glycogen granules. The posterior extremity of the spermatozoon consists solely of the axoneme and enveloping plasma membrane (Fig. 2u). Total sperm length, from phase-contrast microscopy, is 90 to 95 μm for *Calantica* and *Smilium* (Fig. 3a,m), 92 μm for *Scalpellum stearnsi* and 110 μm for *Lithotrya* (Fig. 2w).

### Lepadidae and Heteralepadidae

The spermatozoa of several lepadid species were compared (*Lepas anserifera*, *Lepas anatifera*, *Lepas pectinata*, *Conchoderma auritum*, *Conchoderma virgatum*), but only limited material was available from a single species of heteralepadid (*Heteralepas japonica*).

The acrosome of *Lepas anserifera* is 0.54 to 0.6 μm long and conical, with axial rod material located within a basal invagination (Fig. 3n,p,q). Acrosomes of *Conchoderma virgatum* were swollen, possibly due to the poor condition of the live specimen collected for study. Some transverse sections were obtained which suggest that the acrosomal vesicle of *C. virgatum* is conical, as in *Lepas*. The acrosome was not identifiable in available material of *Conchoderma auritum*. A dense collar is present immediately posterior to the acrosomal region, measuring approximately 0.6 μm in *Lepas anserifera* (Fig. 3n). In transverse section the nucleus of *Lepas* and *Conchoderma* has a sharply defined, triangular profile (Fig. 3u–w). The accessory droplets of *Lepas* and *Conchoderma* are narrow (maximum width 0.4 to 0.6 μm) and contain a prominent rod composed of a dense core (diameter 0.06 to 0.07 μm in *Lepas*, 0.03 μm in *Conchoderma*) surrounded by a narrow space, then a less electron-dense outer layer, 0.05 to 0.06 μm thick in *Lepas* (Fig. 3r,s,v) and 0.07 to 0.08 μm thick in *Conchoderma* (Fig. 3w). Phase-contrast microscopy revealed a droplet length of 28 to 35 μm in *Lepas* and *Conchoderma* (Figs 3o, 4a). From available material of *Heteralepas japonica*, it was possible to determine only that the sperm nucleus is triangular in cross section, and that a rod is probably present in the droplet. In *Lepas* and *Conchoderma*, glycogen granules occur before and after termination of

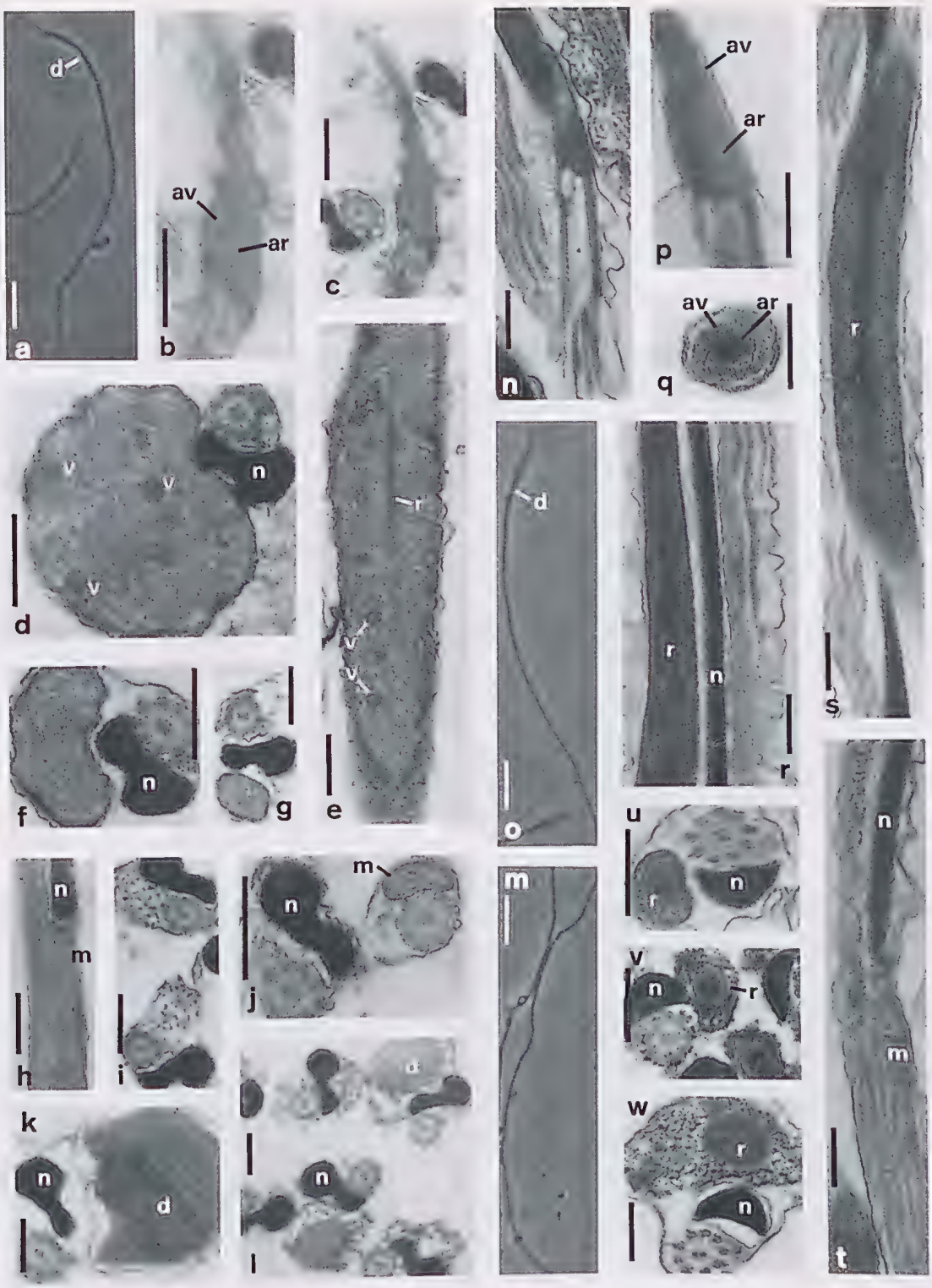


**Fig.3.** (a — n) Scalpellidae (continued). (a — j) *Smilium peronii*. (a) Whole spermatozoon. (b, c) L.S. acrosome. (d) T.S. droplet, nucleus and axoneme. (e) L.S. portion of droplet showing rod and scattered vesicles. (f) T.S. posterior region of droplet. (g) T.S. terminal region of droplet, with associated axoneme, nucleus. (h) L.S. junction of nucleus and mitochondrion. (i) T.S. glycogen region of sperm. (j) T.S. mitochondrial region of sperm. (k) *Calantica spinosa*. T.S. droplet, anoneme and nucleus. (l) *Calantica villosa*. T.S. axoneme, nucleus and droplet. (m) Whole spermatozoon of *Calantica spinosa*. (n — w) Lepadidae. (n — u) *Lepas anserifera*, (n) L.S. acrosome, collar, axoneme. (o) Whole spermatozoon. (p) L.S. acrosome. (q) T.S. acrosome. (r, s) L.S. droplet with thick rod, nucleus, axoneme. (t) Junction of nucleus and mitochondrion (note glycogen deposits). (u) T.S. droplet, nucleus, axoneme. (v) *Lepas anatifera*. T.S. droplet, nucleus, axoneme. (w) *Conchoderma virgatum*. T.S. droplet (note thick rod), nucleus, axoneme. Scale bars: a,o,m = 10 μm; p,q = 0.2 μm; all others = 0.25 μm.

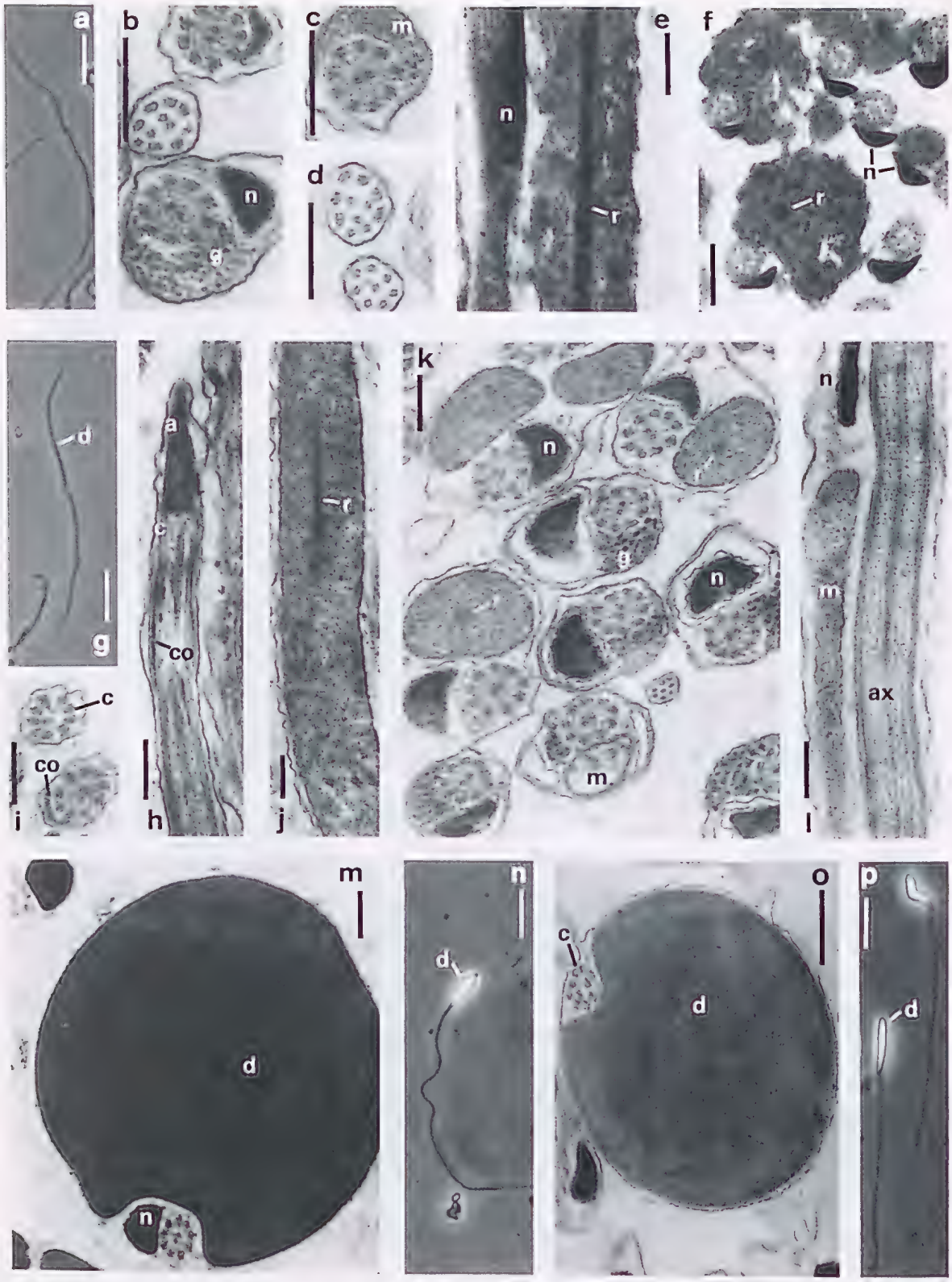


**Fig.4.** (a — d) Lepadidae. (a) *Conchoderma virgatum*, whole spermatozoon. (b — d) *Lepas anserifera*. (b) T.S. anterior region of axoneme and nucleus (top of figure); glycogen region of sperm (bottom), posterior extremity of sperm (middle). (c) T.S. mitochondrial region. (d) Transition of 9 + 2 axoneme into single microtubules at posterior extremity of sperm. (e, f) *Verruca ströemia*. (e) L.S. droplet, with thick rod. (f) T.S. droplet, axoneme and nucleus. (g — p) Balanomorpha. (g — l) *Catomerus polymerus* (Catophragmidae). (g) Whole spermatozoon. (h) L.S. acrosome, collar, centriolar zone, axoneme. (i) T.S. centriole, collar/axoneme. (j) L.S. portion of droplet showing rod. (k) T.S. axoneme/nucleus with droplet, axoneme/nucleus with glycogen granules, axoneme with mitochondrion. (l) Junction of nucleus and mitochondrion, with accompanying axoneme. (m — p) Chthamalidae. (m, n) *Octomeris brunnea*. (m) T.S. droplet, axoneme, nucleus. (n) Whole spermatozoon. (o, p) *Chthamalus antennatus*. (o) T.S. droplet, centriole, nucleus. (p) Whole spermatozoa. Scale bars: a,g,n,p = 10 μm; all others = 0.25 μm.

the accessory droplet (Figs 3t, 4b). These granules are also associated with the single mitochondrion (Figs 3t, 4c) which replaces the nucleus posteriorly. The 9 + 2 axoneme degenerates, first into nine disordered doublets with persistence of the central pair of microtubules, then into single microtubules (see Fig. 4b,d). Spermatozoa of *Lepas* spp. measure 90 to 95 μm, (Fig. 3o) while those of *Conchoderma* spp. (Fig. 4a) are approximately 80 to 85 μm long.

## Verrucomorpha

### Verrucidae (*Verruca ströemia*)

Available material of *Verruca ströemia* was useful only for determining the shape of the nucleus and some features of the accessory droplet. In transverse section, the nucleus has a sharply-defined triangular profile, and the droplet (maximum observed width 0.6 μm) contains a thick rod (Fig. 4f). Longitudinal sections (Fig. 4e) through the droplet suggest the the rod may be composed of two elements, a dense core with a diameter of 0.07 μm and a more electron-lucent enveloping layer about 0.01 μm thick. These and other details of the spermatozoa of *Verruca* will be fully resolved only through a study of better-fixed tissues. Barnes *et al.* (1971) give a length of 6 μm for the droplet of *V. ströemia*, but their photographs suggest that the length may be up to 12 μm.

## Balanomorpha Chthamaloidea

### Catophragmidae (*Catomerus polymerus*)

The acrosomal vesicle of *Catomerus polymerus* is 0.05 μm long, with a basal invagination containing axial rod material (Fig. 4h). A collar 0.7 μm long extends posteriorly from the centriole, sheathing the initial portion of the axoneme (Fig. 4h,i). The centriole is composed of nine doublets (Fig. 4i). Posterior to the collar, the axoneme becomes associated with the nucleus, triangular in transverse section (Fig. 4k), and a long, narrow accessory droplet (length 22 to 25 μm, maximum width 0.7 to 0.8 μm, Fig. 4g,j,k). A single rod lies within the granular matrix of the droplet (Fig. 4j,k). A tract of glycogen granules lies close to the axoneme and nucleus, particularly behind the accessory droplet (Fig. 4k). The nucleus is succeeded by a single mitochondrion possessing typical cristae (Fig. 4k,l). Degeneration of the axoneme into microtubules follows the pattern outlined for *Ibla*.

### Chthamalidae (*Chthamalus antennatus*, *C. malayensis*, *Octomeris brunnea*, *Chamaesipho tasmanica*)

Spermatozoa of chthamalids differ from those of *Catomerus* principally in an increased diameter of the accessory droplet and, in *Chthamalus* and *Octomeris*, a reduced droplet length. Acrosomal morphology was traced only for *Chamaesipho tasmanica*, where the vesicle is conical, 0.5 to 0.6 μm long, and has axial rod material lodged within its invaginated base (Fig. 5a). In this species, the accessory droplet is 17 to 18 μm long (Fig. 5d,e) and up to 1.0 μm wide, and contains a single rod together with electron-lucent areas within the matrix (Fig. 5b,c). The shorter, wider droplets of *Chthamalus* and *Octomeris*, 8 to 11 μm long and up to 2 μm wide, have no rod or other substructural elements (Fig. 4m-p). Sperm nuclei of *Chthamalus*, *Octomeris* and *Chamaesipho* are triangular in transverse profile. Phase-contrast microscopy gave the following lengths for chthamalid spermatozoa: *C. antennatus*, 70 μm; *C. malayensis*, 100 μm; *O. brunnea*, 68 to 70 μm; *C. tasmanica*, 70 to 75 μm, (Figs 4n,p, 5d,e).

## Balanomorpha Coronuloidea

### Coronulidae (*Coronula diadema*, *Chelonibia testudinaria*, *Cylindrolepas darwiniana*, *Tubicinella cheloniae*, *Platylepas coriacea*, *Platylepas hexastylos*)

The acrosomal vesicles of these species are conical with an invaginated base, and range in length from 0.6 to 0.7 μm (*Chelonibia*, *Tubicinella*) to 0.38 μm (*Platylepas*) (Fig. 5g). A collar appears to be present in all species, but in no case could its length be determined. The accessory droplets of *Chelonibia testudinaria* (Fig. 5h–j), *Cylindrolepas darwiniana* (Fig. 5m,n), *Coronula diadema* (Fig. 5o–q) and *Tubicinella cheloniae* (Fig. 5f,k,l) are moderately long (14 to 20 μm) and narrow (markedly so in *Tubicinella* and *Cylindrolepas*). In *Platylepas* spp., the droplet is only 6 to 7 μm long and much wider than in other coronulids (Fig. 5r–t). A rod is present in the droplets of *Chelonibia*, *Tubicinella* and *Cylindrolepas* (Fig. 5h,j,k–m), but lacking in *Coronula* and *Platylepas* (Fig. 5o,p,t). In *Coronula*, *Tubicinella* and probably *Cylindrolepas*, the axial core of the droplet is appreciably less electron-dense than the surrounding area (Fig. 5l,o,p). The nucleus in all coronulid spermatozoa is triangular in cross section, and is succeeded posteriorly by a single mitochondrion. Phase-contrast microscopy gave the following lengths for whole spermatozoa: *Chelonibia*, 48 to 50 μm (Fig. 5i); *Coronula*, 58 to 60 μm (Fig. 5q); *Tubicinella*, 50 μm (Fig. 5f); *Cylindrolepas*, 56 μm; *Platylepas*, 40 μm (Fig. 5r,s).

### Tetraclitidae (*Austrobalanus imperator*, *Epopella plicata*, *Tesseropora rosea*, *Tetraclita squamosa*, *Tetraclitella purpurascens*)

Among the tetraclitids there is variation in the length of the accessory droplet and in its position along the axoneme/nuclear complex, as well as some variation in acrosomal

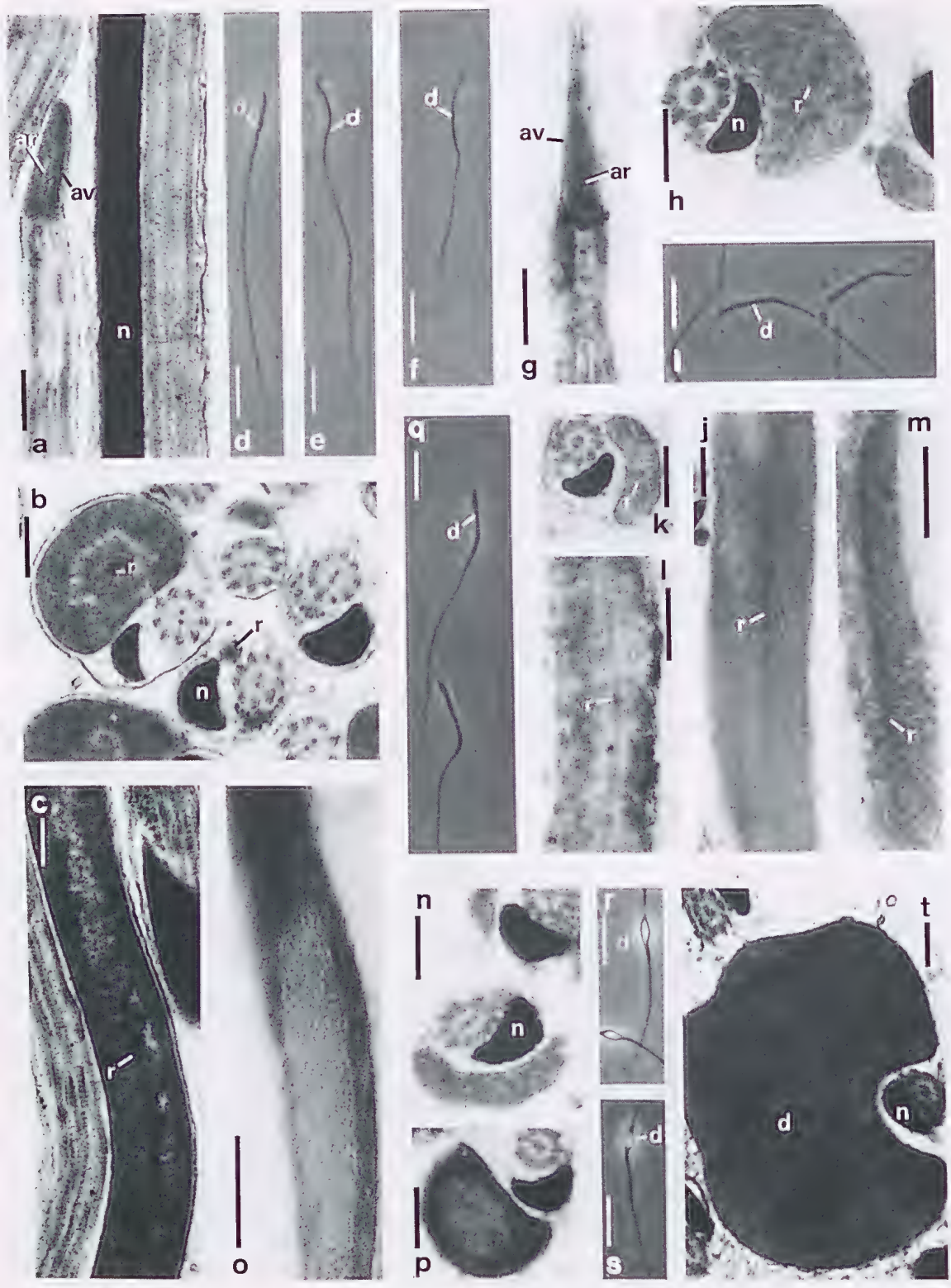


**Fig.5.** Balanomorpha. (a — e) Chthamalidae, *Chamaesipho tasmanica*. (a) L.S. acrosome, collar, axoneme, nucleus. (b) T.S. axoneme/nucleus with accessory droplet and with glycogen (right). (c) L.S. droplet and axoneme. (d, e) Whole spermatozoa. (f — t) Coronulidae. (f) Whole spermatozoon of *Tubicinella cheloniae* (g — j) *Chelonibia testudinaria*. (g) acrosome. (h) T.S. droplet, axoneme, nucleus. (i) Whole spermatozoon. (j) L.S. portion of droplet showing rod. (k, l) *Tubicinella cheloniae*. (k) T.S. droplet, axoneme, nucleus. (l) L.S. portion of droplet showing rod. (m, n) *Cylindrolepas darwiniana*. (m) L.S. portion of droplet with rod. (n) T.S. slightly oblique through droplet, nucleus, axoneme. (o — q) *Coronula diadema*. (o) L.S. portion of droplet with differentiated central zone. (p) T.S. droplet. (q) Whole spermatozoon. (r — t) *Platylepas*. (r) Whole spermatozoon of *Platylepas coriacea*. (s) Whole spermatozoon of *Platylepas hexastylos*. (t) T.S. droplet, axoneme, nucleus of *Platylepas coriacea*. Scale bars: d–f,i,q–s = 10 μm; all others = 0.25 μm.

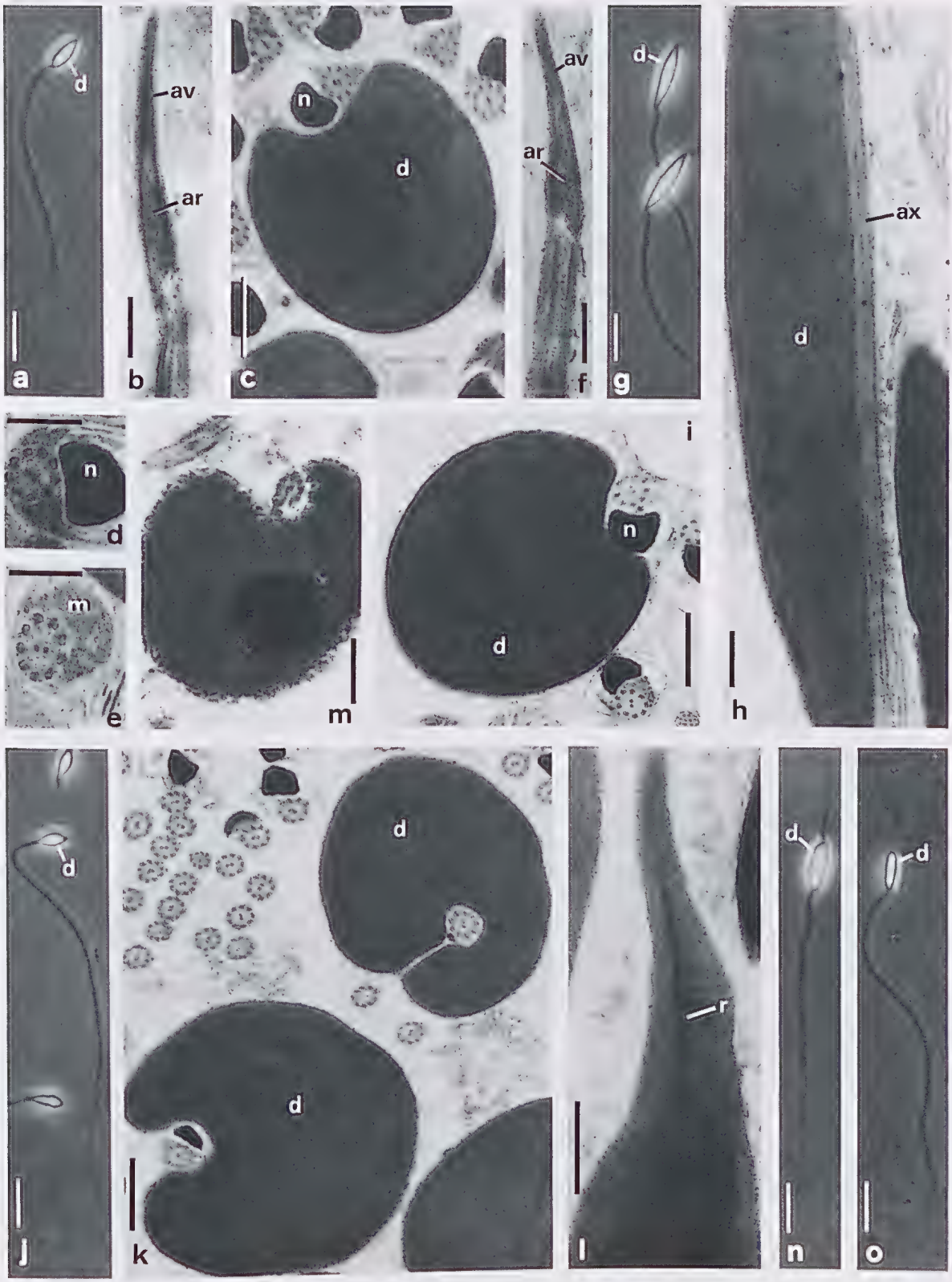


**Fig.6.** Balanomorpha, Tetraclitidae. (a — e) *Tesseropora rosea*. (a) Whole spermatozoon. (b) L.S. acrosome. (c) T.S. droplet, axoneme, nucleus. (d) L.S. glycogen region. (e) T.S. mitochondrial region. (f — i) *Austrobalanus imperator*. (f) L.S. acrosome. (g) Whole spermatozoa. (h) L.S. droplet and axoneme. (i) T.S. droplet, axoneme, nucleus. (j — m) *Epopella plicatus*. (j) Whole spermatozoon. (k) T.S. showing deep enclosure of axoneme/nucleus by droplet. (l) L.S. tapered extremity of droplet. (m) T.S. of droplet. Vesicle-like structure is probably an artefact of droplet degeneration in this spermatozoon. (n) Whole spermatozoon of *Tetraclita squamosa*. (o) Whole spermatozoon of *Tetraclitella purpurascens*. Scale bars: a,g,j,n,o = 10 μm; b,d–f = 0.25 μm; all others = 0.5 μm.

length. In *Austrobalanus imperator* and *Tesseropora rosea* the acrosomal vesicle is long in comparison with other thoracicans, and measures up to 1 μm (Fig. 6b,f). In *Tetraclitella purpurascens* the acrosomal vesicle is about 0.7 μm long (Fig. 7b). Acrosomes were not traced in *Epopella plicata* or *Tetraclita squamosa*. In all species, the accessory droplet is wide, with a groove containing the axoneme and nucleus (Fig. 6c,i,k). Nuclei are triangular in transverse section. In *Epopella*, the axoneme and nucleus may be almost totally enclosed by the droplet at some levels (see Fig. 6k). No evidence of a rod could be found in the droplets of *Tesseropora*, *Austrobalanus*, *Tetraclita* or *Tetraclitella* (Figs 6c,h,i, 7a) but a rod was observed in the droplet of *Epopella*, most clearly at the tapered extremities (Fig. 6l). Kubo *et al.* (1979) mentioned that the droplet of *Tetraclita squamosa* was of 'dual texture', exhibiting spherical, differentiated zones, but we could find no clear evidence of this in our material (sea water/formalin-fixed). Droplet lengths range from 6.5 μm in *Epopella* (Fig. 6j), to 7.5 to 8 μm in *Tesseropora* and *Tetraclitella* (Fig. 6a,o), 10 μm in *Tetraclita* (Fig. 6n) and 14 μm in *Austrobalanus* (Fig. 6g). Whole sperm lengths range from 65 μm in *Austrobalanus* to 75 to 82 μm in the other genera (Fig. 6a,g,j,n,o).

## Balanomorpha Balanoidea

### Archaeobalanidae (*Hexaminius foliorum*, *H. popeiana*; *Elminius covertus*; *Armatobalanus allium*, *A. arcuatus*; *Acasta spongites*)

The spermatozoa of the archaeobalanids examined in the present study showed substantial variation in the length and substructure of the accessory droplet. Spermatozoa of *Hexaminius* and *Elminius* are similar to those of the generalised chthamaloid *Catomerus polymerus*. The acrosomal vesicle measures 0.4 to 0.5 μm and is basally invaginated (Fig. 7d,e,m). A collar 0.7 to 0.9 μm long extends posteriorly from the base of the acrosome, where it then sheaths the centriole and the initial portion of the axoneme (Fig. 7e,j). The accessory droplet is long (17 to 20 μm) and narrow (maximum width 0.6 μm), with a single rod (diameter 0.02 to 0.04 μm) (Fig. 7c,f,i,l,n,o). Nuclei have a triangular transverse profile (Fig. 7h,i,l,o). The axoneme/nucleus complex lies along the weak indentation in the droplet. A single mitochondrion, measuring 2.4 μm in *H. foliorum*, replaces the nucleus posteriorly (Fig. 7g). Glycogen deposits are associated with the axoneme/nucleus, particularly behind the level of the accessory droplet, and the axoneme/mitochondrion (Fig. 7f–h,o). Sperm length is approximately 67 μm in *Hexaminius* and *Elminius* (Fig. 7c,n).

In *Armatobalanus* spp., the droplet is 7 to 8 μm long and 0.7 to 1.0 μm wide, and contains a variable number (8 to 10) of dense spheres, which at the light microscopic level give the droplet a beaded appearance (Fig. 8a,c–g). These spherical vesicles are linked by a single rod (Fig. 8g). The acrosomal vesicle of *Armatobalanus* is short (approximately 0.25 μm) and conical, with its basal invagination filled by axial rod material (Fig. 8b). A collar is present, but is not well developed. Nuclei have a triangular transverse profile (Fig. 8c). A single mitochondrion replaces the nucleus posteriorly (Fig. 8d). Whole spermatozoa of *Armatobalanus* are 52 to 54 μm long (Fig. 8a,e — phase-contrast microscopy).

Spermatozoa of *Acasta spongites* have a droplet which is the same length as in *Armatobalanus* but is much wider, and lacks either a rod or any vesicle substructure (Fig. 8i). The length of the whole spermatozoon is 65 to 67 μm (Fig. 8h).

### Pyrgomatidae (*Pyrgoma cancellata*; *Creusia spinulosa*; *Savignium elongatum*)

Light microscopy clearly shows that the accessory droplets of pyrgomatid spermatozoa are beaded (Fig. 8k,n,o), like those of *Armatobalanus* (Fig. 8a,e). Droplet length varies from 8.5 to 10 μm in *Pyrgoma* and *Creusia* to 16 to 18 μm in *Savignium*. Internally the droplet contains spherical, dense vesicles 0.3 μm in diameter linked by a rod (Fig. 8j,l,m,p). Nuclei remain triangular in transverse section. The lengths of the spermatozoa are as follows: 55 to 57 μm (*P. cancellata*); 75 to 77 μm (*S. elongatum*); 85 μm (*C. spinulosa*).

### Balanidae (*Balanus variegatus*, *B. amphitrite*; *Austromegabalanus nigrescens*; *Megabalanus ajax*)

Considerable variation also exists in the morphology of the accessory droplet and, to some extent, the acrosome of balanid spermatozoa. The acrosome is short in *Balanus variegatus* (0.3 μm, Fig. 9a,b), but longer in *B. amphitrite* (0.56 μm, Fig. 9i–k), *Austromegabalanus nigrescens* (0.54 μm, Fig. 10b) and *Megabalanus ajax* (0.56 μm, Fig. 10m). In all species the acrosome is conical, with axial rod material located within a deep basal invagination. The accessory droplet is narrow and slightly elongate in *B. variegatus* (0.45 x 20 μm, Fig. 9c–e,g) and *B. amphitrite* (0.7 x 17 to 20 μm, Fig. 9h,l,m), with a row of widely separated spherical to oblong vesicles connected by a rod. In *Austromegabalanus nigrescens*, the droplet also shows spherical to oblong vesicles (Fig. 10c–e), very dense in comparison to the surrounding matrix, and a rod (Fig. 10c–d). However the droplet of *A. nigrescens* is much wider (1.8 μm) and shorter (5 to 6.5 μm) than those of *B. variegatus* or *B. amphitrite*, and frequently shows more than one row of vesicles (Fig. 10e). The droplet in *Megabalanus ajax* is very wide (maximum diameter 2.26 to 2.3 μm) and short (6.5 to 7.5 μm). It appears to lack either spherical vesicles or a rod, and has a deep groove which contains the nucleus and axoneme (Fig. 10i–k). Transverse sections show that the profile of the accessory droplet in *M. ajax* is crescentic towards the tapered extremities

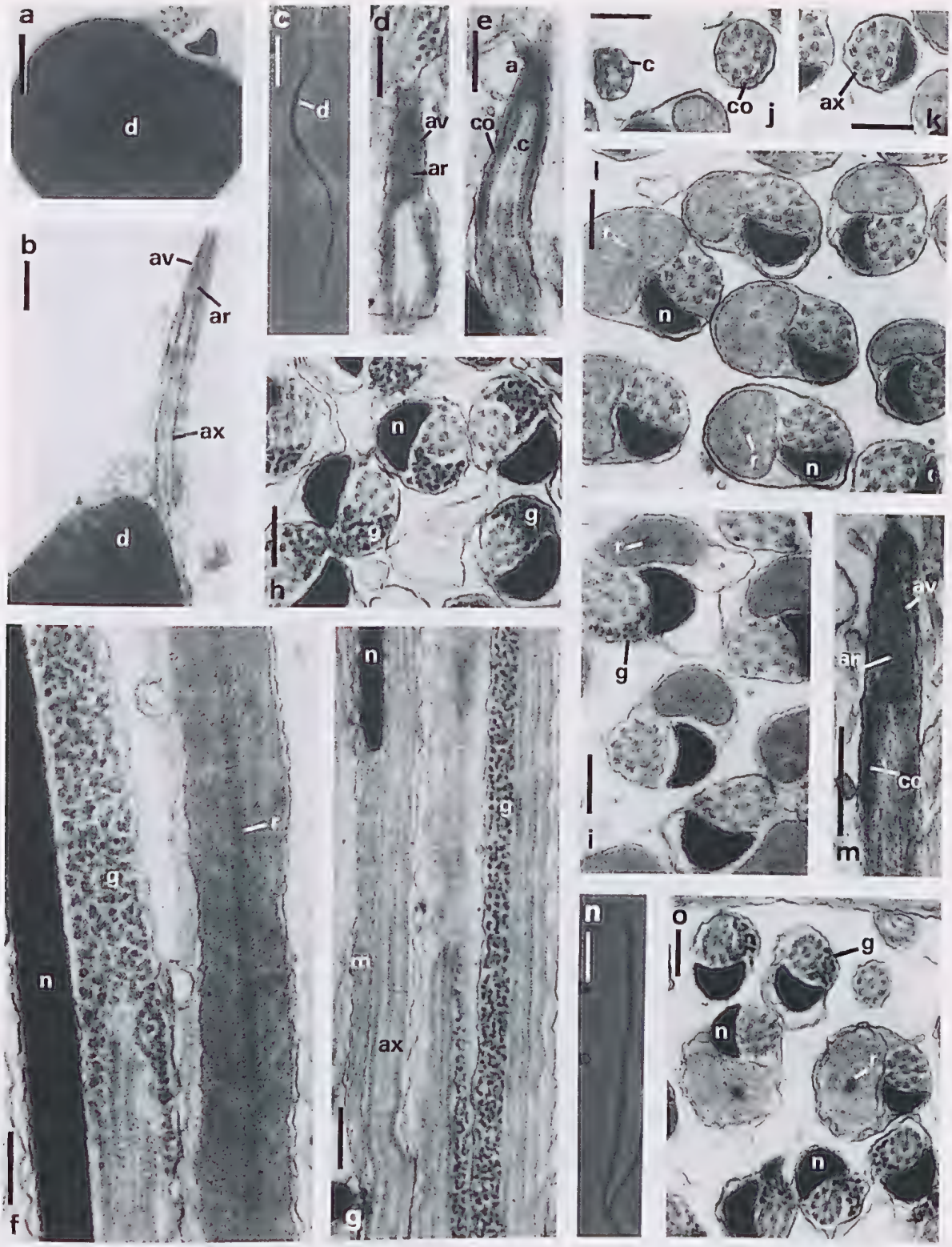


**Fig.7.** Balanomorpha. (a, b) *Tetraclitella purpurascens* (Tetraclitidae). (a) T.S. droplet, axoneme, nucleus. (b) L.S. acrosome, axoneme and anterior extremity of droplet. (c — o) Archaeobalanidae. (c — i) *Hexaminius foliorum* (c) Whole spermatozoon. (d, e) L.S. acrosome, collar, centriole, proximal region of axoneme. (f) L.S. droplet (with rod), nucleus and glycogen granules. (g) L.S. junction of nucleus and mitochondrion (left), glycogen and axoneme (right). (h) T.S. glycogen region. (i) T.S. droplet (with rod), axoneme, nucleus. (j — l) *Hexaminius popeiana*. (j) T.S. centriole (left), axoneme/collar (right). (k) T.S. axoneme and anterior region of nucleus. (l) T.S. droplet, axoneme and nucleus. (m — o) *Elminius covertus*. (m) L.S. acrosome, collar, proximal portion of axoneme. (n) Whole spermatozoon. (o) T.S. droplet and glycogen regions of spermatozoon. Scale bars: c,n = 10 μm; a,b = 0.5 μm; all others = 0.25 μm.

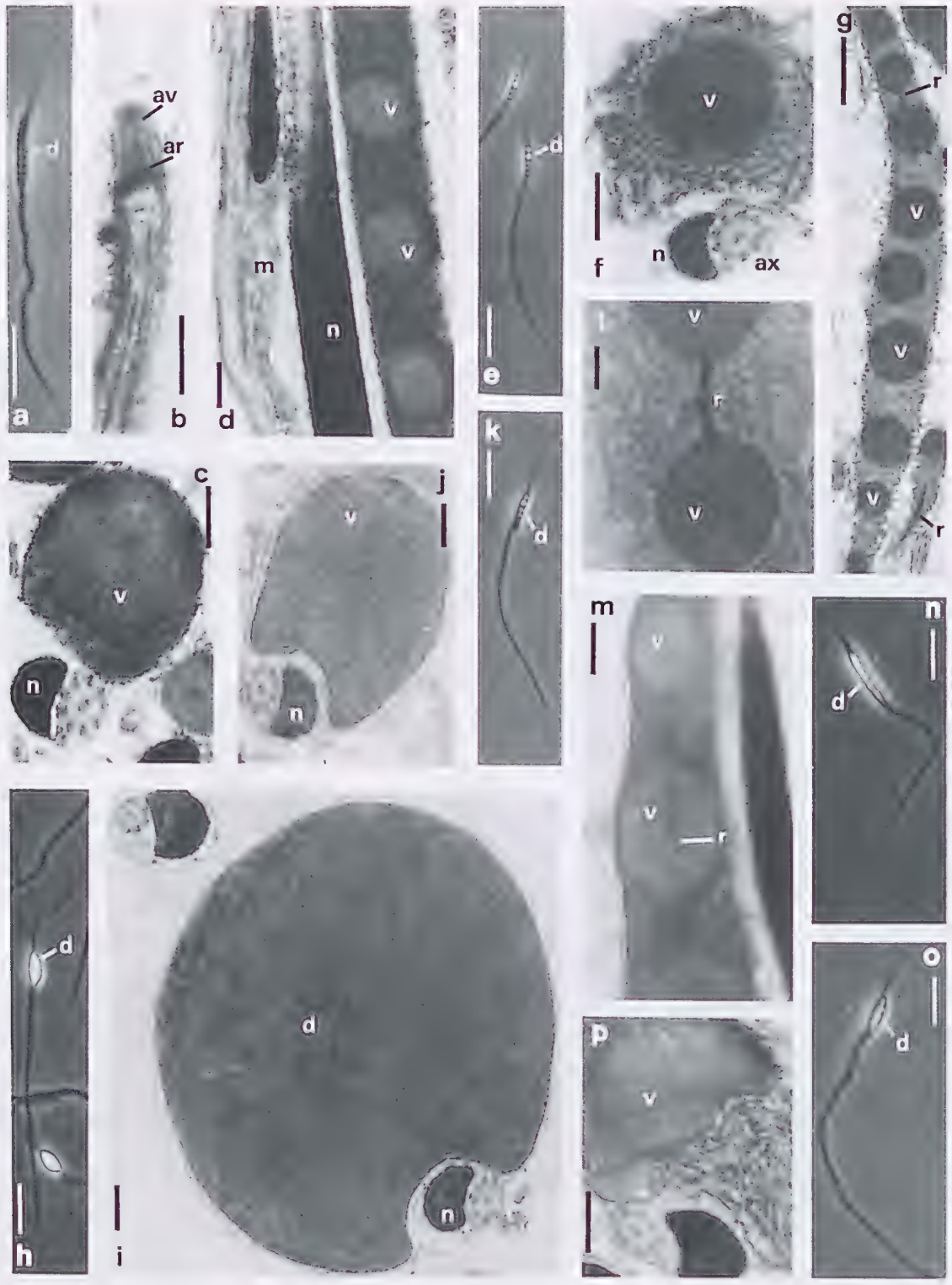


**Fig.8.** Balanomorpha. (a — i) Archaeobalanidae. (a — d) *Armatobalanus allium*. (a) Whole spermatozoon — internal vesicles of accessory droplet visible as beads. (b) L.S. acrosome, collar, proximal portion of axoneme. (c) T.S. droplet (note large internal vesicle). (d) L.S. droplet and nucleus — mitochondrion junction. (e — g) *Armatobalanus arcuatus*. (e) Whole spermatozoon, beading visible in droplet. (f) T.S. droplet with dense vesicle, axoneme, nucleus. (g) L.S. droplet showing vesicles and rod. (h, i) *Acasta spongites*. (h) Whole spermatozoon, absence of beading in droplet. (i) T.S. droplet (no vesicle present), nucleus, axoneme. (j — p) Pyrgomatidae. (j — m) *Pyrgoma cancellata*. (j) T.S. droplet, nucleus, axoneme. (k) Whole spermatozoon, beading visible in droplet. (l) Vesicles of droplet connected and penetrated by rod. (m) Vesicles and rod in droplet. (o, p) *Creusia spinulosa*. (o) Whole spermatozoon, with beading in droplet. (p) T.S. droplet with vesicle, nucleus, axoneme. Scale bars: a = 15 μm; e,h,k,n,o = 10 μm; all others = 0.25 μm.

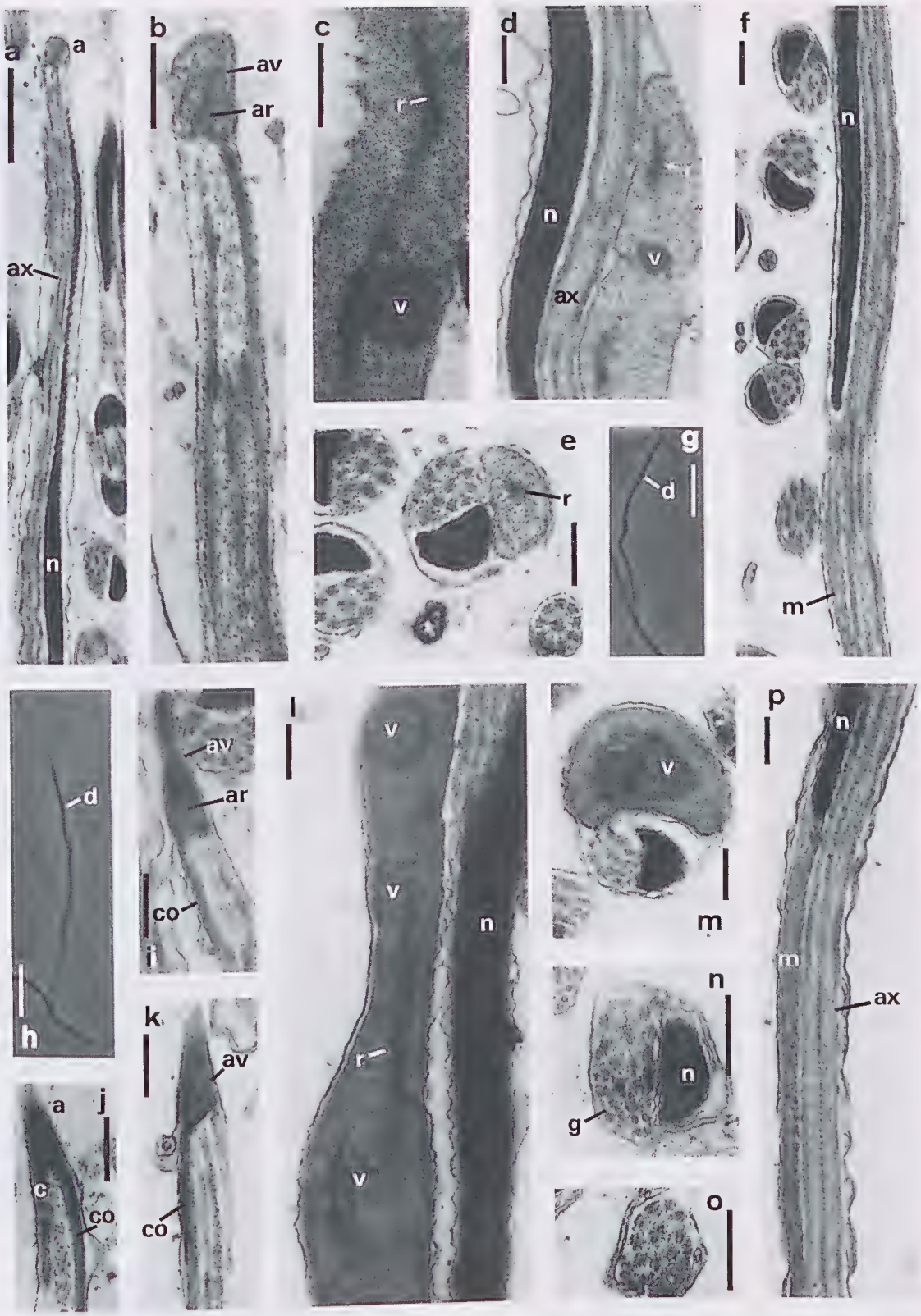


**Fig.9.** Balanomorpha, Balanidae. (a — g) *Balanus variegatus*. (a) L.S. acrosome, axoneme, nucleus. (b) L.S. acrosome, centriole/axoneme/collar region of sperm. (c) L.S. portion of droplet, with rod and dense vesicle. (d) L.S. portion of nucleus, axoneme and droplet, with rod and vesicle. (e) T.S. droplet, axoneme, nucleus. (f) L.S. nucleus — mitochondrion junction. (g) Whole spermatozoon. (h — p) *Balanus amphitrite*. (h) Whole spermatozoon. (i — k) L.S. acrosome, centriole, collar, proximal portion of axoneme. (l) L.S. nucleus, droplet (with rod and vesicles). (m) T.S. droplet, axoneme, nucleus. (n) T.S. glycogen region. (o) T.S. mitochondrial region. (p) L.S. nucleus-mitochondrion junction. Scale bars: g,h = 10 μm; a = 1.0 μm; all others = 0.25 μm.

(Fig. 10l). Balanid sperm nuclei are triangular in transverse section. The lengths of balanid spermatozoa (phase-contrast miscroscopy) are: *B. variegatus*, 52 to 54 µm; *B. amphitrite*, 55 µm; *Austromegabalanus nigrescens*, 50 to 52 µm; *Megabalanus ajax*, 51 to 53 µm (Figs 9g,h, 10a,j).

Figure 11 summarises the variations in shape, position and internal morphology of the accessory droplet among major lepadomorph and balanomorph taxa.

## Discussion

### Thecostracan Spermatozoa

This study, in conjunction with other work on sperm ultrastructure in the Thecostraca (Bocquet-Vedrine & Pochon-Masson, 1969; Turquier & Pochon-Masson, 1969; Brown, 1970; Pochon-Masson *et al.*, 1970; Pochon-Masson, 1971; Munn & Barnes, 1970a, 1970b; Kubo *et al.*, 1979; Azevedo & Corral, 1982; Grygier, 1981, 1982; also Anderson & Personne, 1970; Klepal, 1985), confirms that the Thoracica, Acrothoracica and Rhizocephala share a distinctive type of filiform spermatozoon (Fig. 1c-g), the chief characteristics of which are: (1) a simple, conical acrosome capping the axoneme; (2) a filiform nucleus running parallel to the axoneme; (3) a single, rod shaped mitochondrion posterior to the nucleus; (4) substantial glycogen deposits associated with the axoneme in the posterior half of the spermatozoon. Thoracican and acrothoracican sperm also share a fusiform accessory droplet, often with internal substructural elements, running parallel to the nucleus and axoneme. An accessory droplet has not been documented for rhizocephalan sperm.

This type of sperm differs considerably from the more generalised spermatozoa of acrothoracidans (Grygier, 1981, 1982) and also from the distinctive flagellate sperm of mystacocaridans (Brown & Metz, 1967) and branchiurans (Brown, 1970; Wingstrand, 1972). The typical 'cirripede' spermatozoon presumably originated from an ascothoracidan-like spermatozoon, although spermiogenesis in thoracicans (Bocquet-Vedrine & Pochon-Masson, 1969; Kubo *et al.*, 1979) does not recapitulate an 'ascothoracidan' stage. In other crustaceans such as Decapoda (Pochon-Masson, 1969), Ostracoda (Gupta, 1968; Reger, 1970; Lopez-Camps *et al.*, 1979a; Wingstrand, 1988), Branchiopoda (Wingstrand, 1978) and Copepoda (Brown, 1970; Lopez-Camps *et al.*, 1979b), the spermatozoa lack an axoneme, often have unusual shapes (e.g. the stellate sperm of many decapods and discoidal sperm of some copepods) and are commonly immotile. There does not appear to be a homologue of the accessory droplet of cirripede sperm in any other group of crustaceans, save perhaps for the pseudoacrosome of *Argulus* (Brown, 1970; Wingstrand, 1972). As emphasised by Munn & Barnes (1970b), Barnes *et al.* (1971), Bocquet-Vedrine & Pochon-Masson (1969) and Kubo *et al.* (1979), the accessory droplet of cirripedes is not homologous with the cytoplasmic droplet of immature mammalian sperm. It is, in fact, a distinct Golgi product formed at an advanced stage of spermiogenesis (Kubo *et al.*, 1979). According to Kubo *et al.* (1979) the accessory droplet reacts negatively for lipid, glycolipid, polysaccharide and acid phosphatase, as well as to digestion tests using DNA-ase and RNA-ase. It does, however, appear to contain lipoprotein (Bocquet-Vedrine & Pochon-Masson, 1969). Motility is increased when the droplet is lost, although Barnes *et al.* (1971) and Barnes *et al.* (1977) considered that sperm motility in cirripedes is more dependent on physiological maturity than on structural features. Passage through the pores of the oviducal sac may be difficult or impossible for sperm which retain the droplet (see Walker, 1980 for discussion of the structure of the pores of the oviducal sac in balanomorphs). Probably the accessory droplet serves a nutritional and/or capacitational function.

The present study, together with those of Bocquet-Vedrine & Pochon-Masson (1969), Munn & Barnes (1970b), Kubo *et al.* (1979), Azevedo & Corral (1982) and Klepal (1985), shows that the accessory droplet of cirripede sperm often exhibits internal substructures such as a simple or structured rod, spherical, differentiated zones (sometimes connected to the rod) and more rarely, lacunae, parallel arrays of membranes, coiled tubules (corpuscle) and crystalloid bodies (Fig. 11). These substructural elements, when considered in conjunction with the shape and size of the droplet, may be of phylogenetic importance, as will be discussed below.

It is well known that the droplet in testicular sperm of cirripedes is frequently ovoid compared with the more streamlined droplet of sperm taken from the seminal vesicle (Barnes *et al.*, 1971). Barnes *et al.* (1971) also found that in some balanomorphs such as *Chthamalus stellatus*, the form of the accessory droplet was variable and that shape changes or final loss of the droplet took place abruptly. We have observed that most sperm within the seminal vesicle possess droplets of a characteristic size and shape for each species.

### Cirripede Spermatozoa and Phylogeny

One of the principal aims of this study has been to attempt to evaluate the relevance of sperm morphology to cirripede phylogeny. As indicated earlier and by previous authors (for example Pochon-Masson, 1971; Baccetti, 1979; Grygier, 1981, 1982), the Thoracica, Acrothoracica and Rhizocephala share a similar modification of sperm architecture and are collectively separable from a sister group Ascothoracida, which retain a more generalised sperm (Grygier, 1981, 1982, 1983). Grygier (1987b, 1987c) and Newman (1982, 1987) also list other grounds for recognition of the Ascothoracida as a sister-group.

Newman (1987), in a review of recent investigations bearing on the phylogenetic relationships of the Rhizocephala, has argued for an origin of the Rhizocephala from a mobile, biting stock, closely related to the ancestors of the Cirripedia (= Thoracica and Acrothoracica) within the Thecostraca. Although the shared filiform sperm is evidence of a close relationship

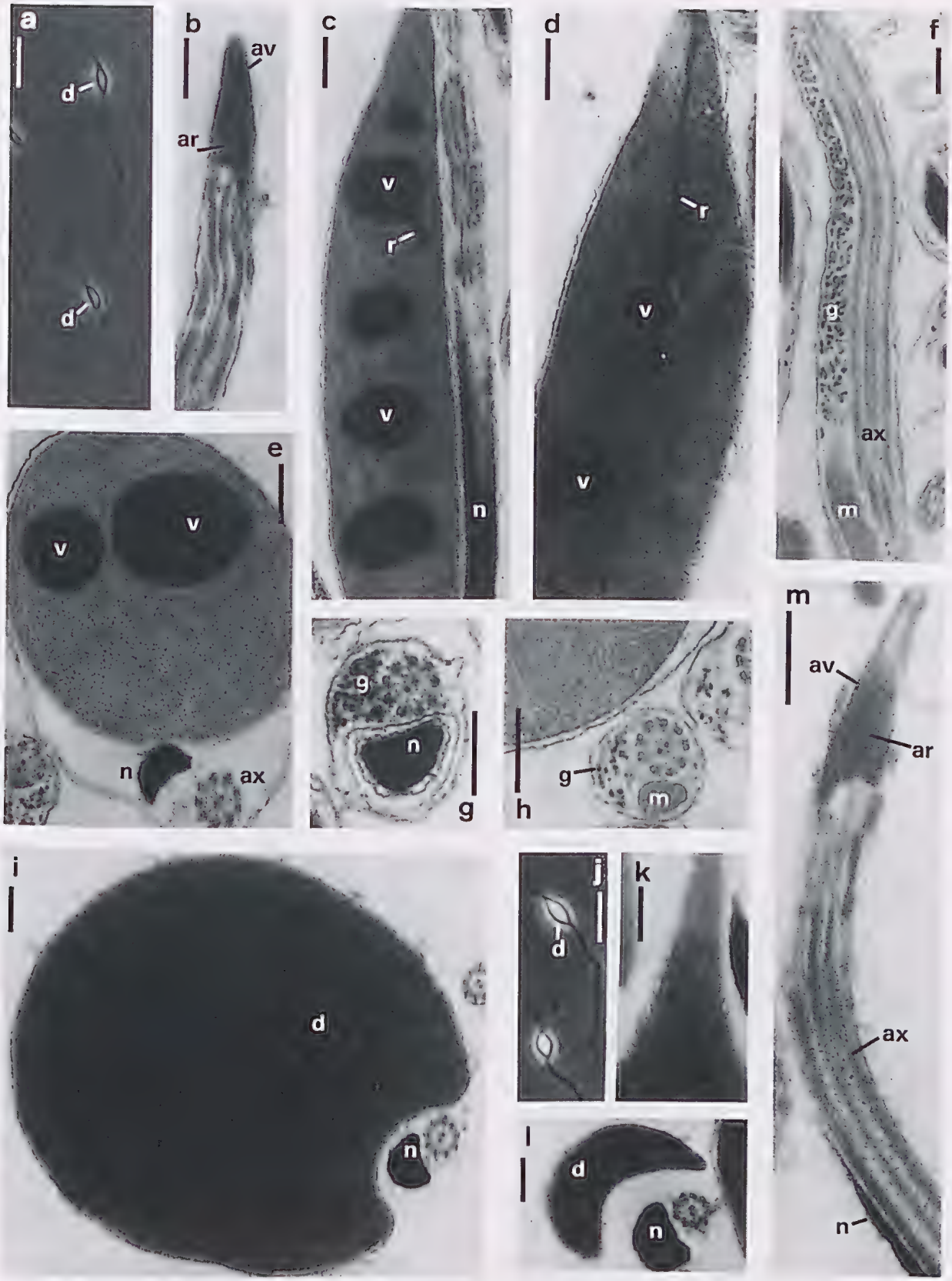


**Fig.10.** Balanomorpha, Balanidae. (a — h) *Austromegabalanus nigrescens*. (a) Whole spermatozoa. (b) L.S. acrosome, collar, centriole, axoneme. (c) L.S. portion of droplet, nucleus, axoneme. (d) L.S. portion of droplet showing rod and vesicle. (e) T.S. droplet, nucleus, axoneme. (f) L.S. glycogen region, axoneme, mitochondrion. (g) T.S. glycogen region. (h) T.S. axoneme, glycogen, mitochondrion. (i — m) *Megabalanus ajax*. (i) T.S. droplet, axoneme, nucleus. (j) Whole spermatozoa. (k) L.S. tapered extremity of droplet. (l) T.S. posterior region of droplet, with axoneme and nucleus. (m) L.S. acrosome, axoneme, nucleus. Scale bars: a,j = 10 μm; c,d = 0.5 μm; all others = 0.25 μm.

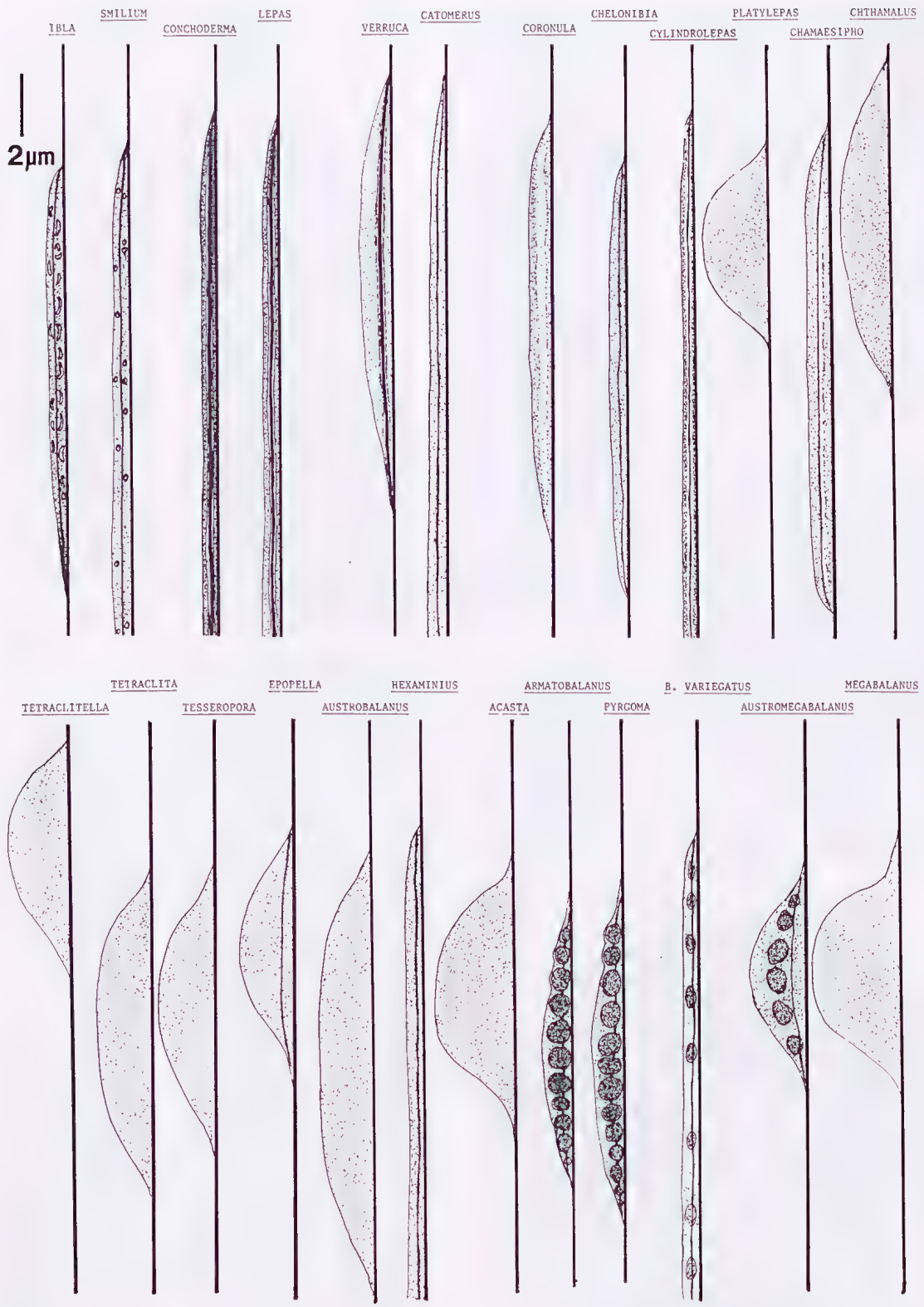


**Fig.11.** Shape, position and substructure of accessory droplet in thoracican spermatozoa relative to anterior portion of spermatozoon (diagrammatic). Acrosomes are not shown: only anterior portions of elongate droplets are illustrated. Substructural elements of droplets include: curved lacunae (*Ibla*); dense vesicles (small — *Smilium*; large — *Armatobalanus*, *Pyrgoma*, *Balanus variegatus*, *Austromegabalanus*); rods (thick, structured — *Lepas*, *Conchoderma*, *Verruca*; thin — many examples). Note: narrow droplets (with rod) in lepadomorphs, and some balanomorphs (*Catomerus*, some coronuloids, the archaeobalanids *Hexaminius* and *Elminius*); wide, shorter droplets, lacking any substructural elements, in other coronuloids and some balanoids; similarity between droplets of *Armatobalanus* and pyrgomatids.

between the Thoracica, Acrothoracica and Rhizocephala, the nuclear transverse profile of the sperm is distinctive in each group. That of thoracicans is triangular (Fig. 12), that of acrothoracicans, dumb-bell shaped (Tomlinson, 1969; Pochon-Masson *et al.*, 1970; Pochon-Masson, 1971; this account) and that of rhizocephalans, crescentic (*Sacculina*, *Clistosaccus*; Pochon-Masson, 1971; J. Hoeg, personal communication). An early divergence of the three groups is therefore indicated. The shared basic structure of the accessory droplet of the thoracicans and acrothoracicans adds another feature to the extensive morphological, developmental and fossil evidence in favour of a divergence of Thoracica and Acrothoracica from a common, sessile, cirripede ancestry (Newman, 1987).

The club-shaped nuclear profile of calanticine sperm, while similar in some respects to the acrothoracican profile, appears to be a modification of the asymmetrical pattern found in *Scalpellum* (Fig. 12). Except for these modifications, a triangular nuclear profile is characteristic of thoracican sperm, including the Ibloidea.

## Thoracican Phylogeny

The complexities of phylogenetic evolution within the Thoracica have become well recognised in recent years (Newman & Ross, 1976; Zevina, 1978, 1981, 1982; Anderson, 1981; Newman, 1982, 1987; Buckeridge, 1983; Foster & Buckeridge, 1987; Newman & Hessler, 1989). In Figs 11 to 13, we have attempted to interpret the possible significance of the patterns of ultrastructure of the accessory droplets of thoracican spermatozoa in relation to current views on thoracican phylogeny. For the most part, the data are confirmatory of these views, although some unexpected problems have arisen.

Taking account of a condition shared with Acrothoracica, we make the assumption that the basic form of the thoracican accessory droplet is that retained in *Pollicipes* (Azevedo & Corral, 1982), *Catomerus*, *Chelonibia*, *Hexaminius* and *Elminius* (this account) and *Semibalanus balanoides* (Munn & Barnes, 1970b). The droplet is long and narrow, with a crescentic transverse profile, and contains a thin, central rod within a uniform granular matrix.

Among lepadomorphs, *Ibla cumingi* and *I. quadrivalvis* are immediately distinguished from all other thoracicans in having a unique droplet substructure (Klepal, 1985; this account; Figs 12, 13). This is in accord with the view that ibloids, with their four plated capitulum, postoral adductor scutorum (Darwin, 1851; Klepal, 1985) and generalised larval musculature (Anderson, 1987) diverged early from other thoracicans (Newman, 1982, 1987).

For non-ibloid lepadomorphs other than scalpellids, data on the accessory droplet are still limited. Heteralepadids appear to retain the basic sperm structure, as might be expected if they occupy the basal status proposed by Foster (1978), but this needs to be confirmed. Lepadids, in contrast, have a modified rod, with a dense core separated by a space from a less dense peripheral sheath. A similar rod has evolved convergently in *Scalpellum* (Scalpellidae) and in the *Verrucomorpha* (see below). The scalpellids provide useful evidence that variations in droplet structure are of phylogenetic value, in that consistent differences are recognisable between major subfamilies (classification of Zevina, 1981), supported by differences in nuclear transverse profile (Fig. 12). While the Pollicipedinae retain the basic condition, there are distinctive and different modifications of droplet and/or nuclear structure in the Lithotryinae (*Lithotrya*), Scalpellinae (*Scalpellum*) and Calanticinae (*Calantica*, *Smilium*). On present evidence, these modifications offer no indications of relationships between the subfamilies. Darwin (1854), on morphological grounds, favoured the Pollicipedinae as close relatives of the scalpelloid ancestors of the Balanomorpha. Newman (1987) has pointed out the difficulties of a direct derivation of balanomorphs from pollicipedine scalpelloids and has demonstrated an evolutionary route from a core scalpelloid stock via the Brachylepadomorpha. At the same time, Newman continues to recognise the closeness of *Pollicipes* to the core stock of scalpelloids, and thus to the balanomorphs, a view previously supported by Anderson (1983) from functional morphology and more recently by Egan & Anderson (1989) from larval comparisons.

The Verrucomorpha are another group with origins among the Brachylepadomorpha, independently of the Balanomorpha (Newman, 1987; Newman & Hessler, 1989). The limited data presented here on sperm ultrastructure in *Verruca* are in accord with the distinctiveness of the Verrucomorpha (Fig. 12). The basic triangular nuclear profile is retained but the accessory droplet is modified through shortening and the development of a complex rod with a thick, dense core, closely covered by a less dense sheath. A somewhat similar rod is found in the elongate droplet of *Scalpellum* sperm, but the sperm nucleus of *Scalpellum* is modified in transverse profile. Sperm morphology does not support earlier suggestions of a calanticine (Newman *et al.*, 1969; Newman, 1982; Buckeridge, 1983) or lithotryine-calanticine (Newman, 1982) origin for the Verrucomorpha.

The broad outlines of the phylogenetic evolution of the Balanomorpha were elucidated by Newman & Ross (1976) and have been refined in certain details in subsequent work (Anderson, 1981, 1987; Anderson & Buckle, 1983; Buckeridge, 1983; Anderson & Anderson, 1985; Foster & Buckeridge, 1987; Newman, 1982, 1987; Egan & Anderson, 1988, 1989) but various problems remain. The relationships of the basic balanomorph stocks Chionelasmatoidea, Pachylasmatoidea and catophragmid Chthamaloidea to each other and to the ancestry of the Balanomorpha are not fully resolved. The origin of the Coronuloidea and the later routes of divergent evolution of the tetraclids and, independently, the Balanoidea from the coronuloid stock are also in need of further elucidation. Within the Balanoidea, there are also indications, particularly from functional morphology (Anderson & Southward, 1987), that the Archaeobalanidae and Balanidae as presently defined may be polyphyletic groupings.

The sperm data of the present work (Fig. 13) are largely in accord with current interpretations of balanomorph

evolution. They also offer some pointers towards the solution of remaining problems. These will be mentioned as we review the summary presented in Figures 11 and 13.

Among early balanomorphs, no sperm data have yet been obtained for *Chionelasmus* or *Pachylasma*. We predict the retention of the generalised structure seen in *Catomerus* and *Chelonibia* and thus a typical symplesiomorphic situation of no elucidatory value. Within the Chthamaloidea, however, the sperm data are more revealing, in separating *Chamaesipho*, in which an elongate droplet is retained but has a distinctive substructure, from the *Octomeris — Chthamalus* line of evolution, with a short, swollen droplet lacking a rod. Other evidence that *Chamaesipho* has evolved from a catophragmid ancestry independently of the other chthamalids is available from larval studies (Egan & Anderson, 1989) and adult morphology (Foster & Newman, 1987; D.T.Anderson, in preparation).

For the Coronuloidea, the lack of sperm data on the Bathylasmatidae presents a serious problem (see below), but interesting trends emerge in the Coronulidae and Tetraclitidae. In the former, several divergent modifications can be traced from the basic thoracican sperm type retained in *Chelonibia*. *Platylepas* presents another example of the shortened, swollen droplet, lacking a rod, previously encountered in the chthamalids. This form of droplet has evolved independently several times (see Fig. 13) and is not, of itself, a useful indication of relationships at higher phylogenetic levels. Within the Coronulidae, however, it serves to separate *Platylepas* from the other genera for which we have sperm data. *Coronula* also lacks a rod, but retains a relatively long, narrow droplet, with an electron-lucent core. Droplets with an even narrower, crescentic transverse profile, retaining a rod, unexpectedly link the *Tubicinella* of turtles with *Cylindrolepas*. On morphological grounds, Monroe (1981) derived *Cylindrolepas* from *Platylepas* and *Platylepas* from *Coronula*, all within the Coronulinae, and placed *Tubicinella* in a separately derived subfamily, Xenobalaninae. The sperm data suggest that phylogenetic evolution within the Coronulidae may be in need of further study.

The Tetraclitidae, on the other hand, share a derived pattern of sperm ultrastructure in which the droplet is short, swollen and, except in *Epopella*, rodless. In the absence of suitable data on the Bathylasmatidae, we are in doubt about the origin of the tetraclitid sperm pattern. The arrows in Figure 13 tentatively reflect relationships based on functional morphology (Anderson & Anderson, 1985) and, except for a different view of tetraclitellan relationships, those of Foster & Buckeridge (1987) derived from palaeontology. Synapomorphies of sperm ultrastructure (this account) and larval development (Egan & Anderson, 1989) fully support the proposal by Newman & Ross (1976) that *Austrobalanus imperator* is a 'six-plated tetraclitid'.

The concept of an origin of the Balanoidea from bathylasmatid coronuloids (Newman & Ross, 1976) has also found further support in recent studies on larval development (Egan & Anderson, 1989). At present we have no sperm data on the bathylasmatids, but can recognise that a number of archaeobalanid genera (*Hexaminius* [Fig. 13], *Elminius*, *Semibalanus*) retain the generalised thoracican sperm. Within the Archaeobalanidae, we are much in need of data on sperm ultrastructure in *Solidobalanus*, *Chirona*, *Membranobalanus* and *Conopea*, but can point to some striking divergences. *Acasta*, for example, is an archaeobalanid in which the accessory droplet displays a short swollen form lacking internal substructure. Since *Acasta* is now known (D.T. Anderson, unpublished) to retain a mode of cirral extension feeding of a very generalised kind, involving prolonged cirral extension together with particle capture by individual rami, the evolutionary origin and phylogenetic relationships of this "archaeobalanid" genus become matters of great interest. The coral-associated genus *Armatobalanus*, on the other hand, is distinctive among archaeobalanids in the possession of prominent vesicles within the sperm accessory droplet, giving it a beaded appearance at the light microscope level (Figs 11, 13). The same beaded modification characterises the coral-inhabiting Pyrgomatidae (e.g. *Creusia*, *Pyrgoma*, *Savignium*), supporting the proposal of Ross & Newman (1973) that *Armatobalanus* might be closely related to the ancestors of the pyrgomatids. A similar dense vesicle substructure, although not obvious as beads under light microscopy, occurs in the accessory droplet of the sperm of certain species of *Balanus* (*B. amphitrite*, *B. variegatus*, this account; *B. trigonus*, Kubo *et al.*, 1979), and may be indicative of a relationship of these *Balanus* "groups" (*sensu* Newman & Ross, 1976) to *Armatobalanus*. The group of *Balanus balanus*, in contrast, lacks this beaded arrangement and has a somewhat swollen accessory droplet in which the dense central rod is surrounded by a less dense sheath (Munn & Barnes, 1970b). The accessory droplet of *B. perforatus* is also wide and contains a rod, but is distinguished by a 'crystalloid corpuscle', a spherical body comprised of tubules (Bocquet-Vedrine & Pochon-Masson, 1969; Munn & Barnes, 1970b). These patterns, distinct from each other and from the configuration of the droplet shared between *B. trigonus*, *B. amphitrite* and *B. variegatus*, raise in another form the question posed by Anderson (1981) on the basis of differences in patterns of cirral activity: is the presently recognised genus *Balanus* (*sensu stricto*, Newman 1979) an assemblage of groups with more than one origin among the archaeobalanids?

Newman (1979) recognised the subfamily Megabalaninae, comprising warm water (*Megabalanus*) and austral (*Austromegabalanus*, *Notomegabalanus*) subgroups, but did not comment on possible affinities with other balanids. Newman & Ross, (1976) had previously hinted at a derivation of *Megabalanus* (*sensu lato*; now the megabalanines) from the group of *Balanus perforatus*. Some features of cirral structure and activity also suggest this relationship (Anderson & Southward, 1987). Comparative sperm ultrastructure (Figs 11, 13) reveals a short, wide, featureless accessory droplet in *Megabalanus* (*M. ajax*, *M. tintinnabulum*; this account, Kubo *et al.*, 1979), convergently like that of the archaeobalanid *Acasta*; and a less swollen droplet in *Austromegabalanus nigrescens*,

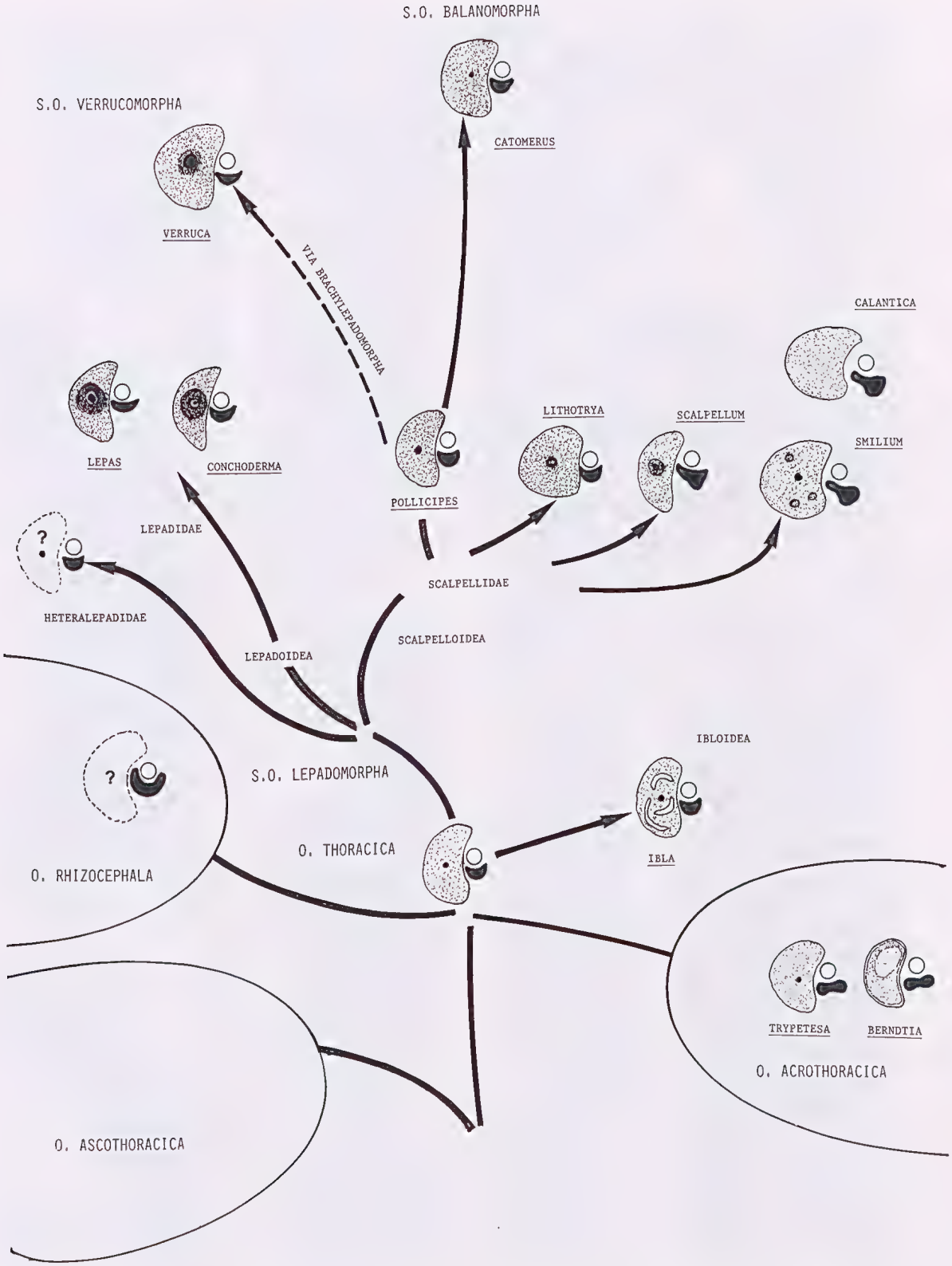


**Fig.12.** Phylogeny of cirripede sperm. Part 1 — Ascothoracida, Rhizocephala, Acrothoracica and Thoracica (Lepadomorpha). Spermatozoa of the Ascothoracida (see Fig. 1a,b) are relatively unmodified in comparison to the filiform spermatozoa of the Rhizocephala, Acrothoracica and Thoracica. Presence or absence of an accessory droplet in Rhizocephala has yet to be established. Nuclear profiles in Rhizocephala (crescentic) and Acrothoracica (dumb-bell shaped) differ from those of thoracicans (triangular). Among lepadomorphs, lepadids are distinct from scalpellids — the latter showing variation in nuclear profile and droplet substructure in different subfamilies. Verrucomorphs were probably derived via the Brachylepadomorpha from a scalpelloid source.

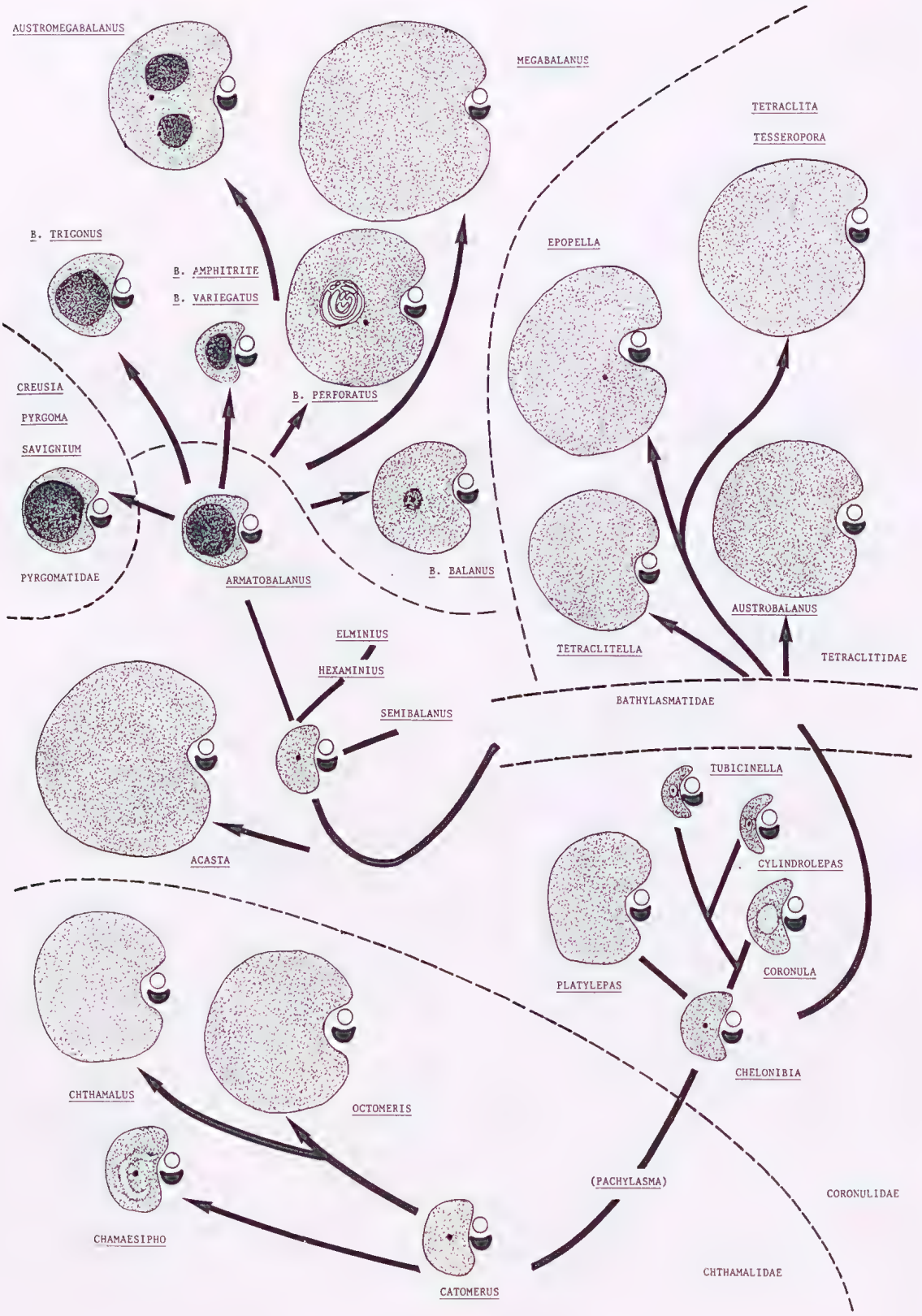


**Fig.13.** Phylogeny of cirripede sperm. Part 2 — Thoracica (Balanomorpha). The sperm of *Catomerus* represents basic balanomorph sperm structure. Repeated trends toward loss of the rod and increase in diameter of the droplet are evident through the Balanomorpha. The basic sperm type is retained in some coronuloids (e.g. *Chelonibia*) and some archaeobalanids (e.g. *Hexaminius*, *Elminius*, *Semibalanus*). Other archaeobalanids show marked divergences in sperm structure, raising the question of whether this is a heterogeneous assemblage. Close links are evident between *Armatobalanus* and the Pyrgomatidae, and with certain balanid taxa. Differences between *Megabalanus* and *Austromegabalanus* are pronounced, suggesting that they may not be closely related to each other.

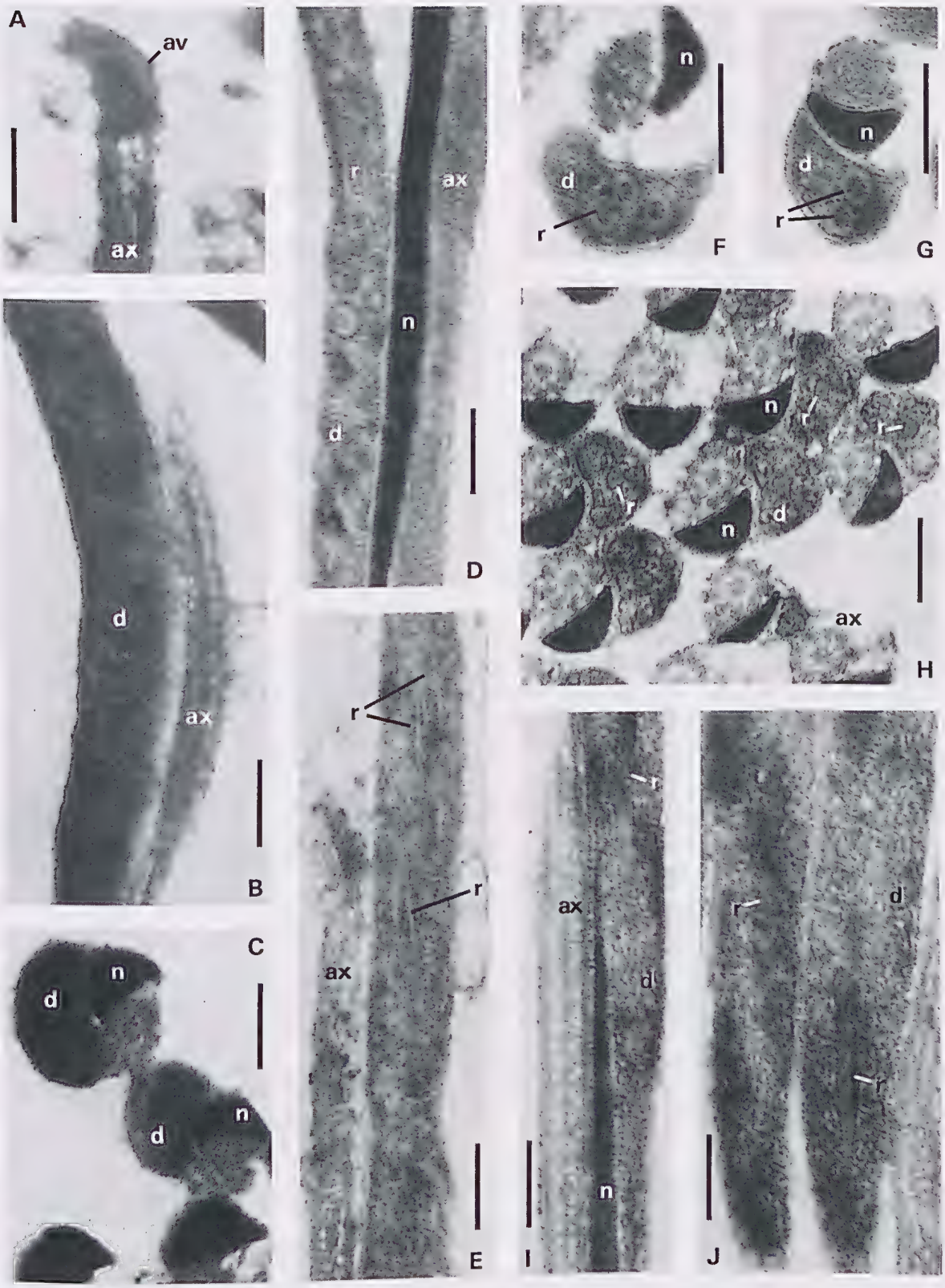


**Fig.14.** (a — c) *Neolepas zevinae*. (a) L.S. acrosome and anterior extremity of axoneme. (b) L.S. accessory droplet and axoneme. (c) T.S. showing droplet, axoneme and nucleus of two spermatozoa. (d — g) *Neoverruca brachylepadoformis*. (d) L.S. showing nucleus, axoneme and droplet. (e) L.S. droplet. Two rods and electron- lucent spaces are visible. (f) T.S. droplet, showing five rods, nucleus and axoneme. (g) T.S. droplet with two rods, nucleus and axoneme. (h — j) *Eochionelasmus* sp. (h) T.S. spermatozoa showing droplet (one rod and a fibrous reticulum), nucleus and axoneme. (i) L.S. droplet, nucleus and axoneme. (j) L.S. droplets of two spermatozoa. Scale bars: 0.25 μm.

with a complex internal substructure of one or two rows of dense vesicles and a separate rod. While a relationship of *Megabalanus* to *B. perforatus* is conceivable on this basis, it seems likely that the austral megabalanines are distinct and perhaps separately derived. Much more needs to be known of all aspects of comparative balanoid biology before the complex phylogenetic evolution of the Balanoidea is fully elucidated.

## Addendum

Since submitting this paper for review, we have had the opportunity to examine spermatozoa from the seminal vesicles of three important thoracicans from the fauna associated with hydrothermal vents, *Neolepas zevinae* Newman, *Neoverruca brachylepadoformis* Newman & Hessler, and *Eochionelasmus* sp. The specimens were kindly provided by Professor W.A. Newman of the Scripps Institution of Oceanography, California, U.S.A. and had been fixed in formalin before transfer to 70% ethanol. The results are illustrated in Fig. 14.

The spermatozoon of *Neolepas zevinae* has a triangular nuclear transverse profile and an elongate accessory droplet about 0.43 µm wide, containing finely granular, homogenous material (Fig. 14a–c). No rod could be detected in the droplet.

The spermatozoan of *Neoverruca brachylepadoformis* (Fig. 14d–g) also retains a triangular transverse nuclear profile and an elongate droplet about 0.40 µm wide, but the droplet contains several rods, each composed of a dense core and an electron-lucent outer layer.

The spermatozoon of *Eochionelasmus* (Fig. 14h–j) has a similar nuclear profile and elongate droplet, but with only a single, simple rod in the centre of the droplet.

All three species thus exhibit the generalised thoracican nuclear profile. *Eochionelasmus* also retains a generalised droplet substructure, but the droplets in *Neolepas* and *Neoverruca* are interestingly distinctive. If the absence of a rod is not a result of poor fixation, *Neolepas* is divergent in this respect from the generalised condition retained in *Pollicipes* and *Lithotrya*. The multiple, distinctive rods of *Neoverruca* have not been observed in any modern scalpelloid, but resemble the specialised single rod in the droplet of *Verruca*.

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# Salticidae (Araneae) of Oriental, Australian and Pacific Regions, IV. Genus *Ocrisiona* Simon, 1901

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ABSTRACT. The spider genus *Ocrisiona* Simon is revised. Eight species are diagnosed, described and illustrated, five new ones are established: *O. eucalypti, O. koahi, O. parmeliae, O. victoriae* and *O. yakatunyae*. Four species, *O. aerata* (L. Koch), *O. elegans* (L. Koch), *O. frenata* Simon and *O. parallelistriata* (L. Koch), are excluded as not related, three additional ones, *O. complanata* (L. Koch), *O. fusca* (Karasch) and *O. invenusta* (L. Koch), are transferred to *Holoplatys*. The genus is redefined and its relationships are discussed. Remarks on biology are presented, maps of distribution and key to the species are given. Geographical distribution of *Ocrisiona* is limited to Australia and adjacent areas; *O. leucocomis* (L. Koch) and *O. melanopyga* Simon are mainland species also recorded from Tasmania, and *O. melancholica* (L. Koch) is also known from Lord Howe Island.

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Since its original description the taxonomy of *Ocrisiona* has not been studied. One species was illustrated by Prószynski (1984) but without any further comments. The synonymisation of the genus with *Holoplatys* (Prószynski, 1987) was premature. Simon (1901a) provided the first clear diagnosis of the genus based upon morphological criteria, but even his taxonomic decisions were partly wrong. From among 12 species of *Ocrisiona* listed by Bonnet (1958) three of Koch's species — *O. aerata, O. elegans* and *O. parallelistriata* — and *O. frenata* Simon (1901b) should be excluded as they represent other taxa. The type specimens of *O. cinerea* and *O. liturata* cannot be found but their original descriptions suggest that both should be transferred to *Holoplatys*, as well as *O. complanata, O. fusca* and *O. invenusta*.

## Material and Methods

The work is based on type specimens listed by Prószynski (1971) and on new material deposited in the

museums listed below. For *O. melancholica* and *O. melanopyga* type specimens have not been found. For each species five specimens of each sex from different localities were measured (in mm), if available. Measurements are given as a range and mean (in brackets). The details on terminology and measurements are illustrated in Fig. 1. Spination of tibia and metatarsus I and II are given as useful taxonomic characters both at specific and generic level; the format of their description follows Platnick & Shadab (1975). The specific names of new species (except *O. eucalypti*) are derived from the type localities.

Collections studied are: AMS — Australian Museum, Sydney; QMB — Queensland Museum, Brisbane; TMH — Tasmanian Museum and Art Gallery, Hobart; WAMP — Western Australian Museum, Perth; MNHN — Muséum National d'Histoire Naturelle, Paris; ZMH — Zoologisches Institut und Zoologisches Museum Universität, Hamburg.

Abbreviations used are: AEW — anterior eyes width; ag — accessory gland; AL — abdomen length; ALE — anterior lateral eyes; CL — cephalothorax length; CW — cephalothorax width; dh — distal haematodocha; e — embolus, EFL — eye field length; fd — fertilisation duct; id — insemination duct; PEW — posterior eyes width; PLE — posterior lateral eyes; s — spermatheca; sr — seminal reservoir; t — tegulum; ta — tibial apophysis.

## Key to the Species of *Ocrisiona*

Males

1. Abdomen with large pale patches posteriorly. Tibia I with single distal prolateral spine ..... *O. melancholica*

—— Abdominal pattern and leg spination not as above ..... 2

2. Abdomen with 2 or 3 pairs of yellow spots alongside a pale median stripe. Anterior abdominal scutum indistinct but present ..... *O. leucocomis*

—— Abdominal pattern not as above, scutum absent ..... 3

3. Embolus longer than tegulum, distal haematodocha reduced ..... *O. yakatunyae* n.sp.

—— Embolus shorter than tegulum, distal haematodocha large ..... 4

4. Palpal tibia short and wide, tibial apophysis large, bent laterally. Cephalothorax with longitudinal median stripe of white hairs, no spines on tibia II ..... *O. parmeliae* n.sp.

—— Palpal tibia longer than wide, tibial apophysis smaller, medial stripe only on thoracic part of cephalothorax, tibia II with one distal prolateral spine ..... *O. victoriae* n.sp.

Females

1. Robust spiders, 3 pairs of spines on tibia I, insemination ducts of epigyne broad, in the shape of reversed "U" ..... *O. melanopyga*

—— Body form more slender, at most 2 pairs of spines on tibia I ..... 2

2. Abdomen with large vast light patches posteriorly. Tibia II with single distal prolateral spine ..... *O. melancholica*

—— Abdominal pattern and leg spination different ..... 3

3. Abdomen with 2 or 3 pairs of yellow spots alongside a pale mid-dorsal stripe ..... *O. leucocomis*

—— Abdomen not as above ..... 4

4. Cephalothorax with longitudinal median stripe, abdominal pattern as in Fig. 10A ..... *O. koahi* n.sp.

—— No median stripe on cephalothorax. Small clusters of white hairs around fovea and behind PLE ..... *O. eucalypti* n.sp.

## Taxonomic Survey

### *Ocrisiona* Simon, 1901

*Marptusa* [part] L. Koch, 1879 : 1100.
*Ocrisiona* Simon, 1901a: 595, 602, 604, 608.

**Diagnosis.** Flat, 'unident', generally dark spiders. Thoracic part of cephalothorax elongated, rather wide. Compared to *Holoplatys* no cephalic depressions between PLE. Legs usually heavily haired, especially in males. Legs I the strongest, legs IV the longest, legs III the shortest or as long as legs II. Tibial spines on legs I and II always present. Male palpal organs with long, thin embolus. Lateral tibial apophysis often with small protuberance, no dorsal apophysis. The epigynal pattern is an inverted heart shape.

**Description** (Fig.1). Medium to large spiders, body length 6–15 mm. Cephalothorax robust, flat and wide, much wider than the distance between posterior lateral eyes, black, often with median or marginal belts of white hairs. Compared to *Holoplatys* no cephalic depressions between PLE. Abdomen black or brown with pattern of white hairs or light patches characteristic for each species. Spinnerets brown to black. Clypeus narrow, sometimes heavily haired but without distinctive fringe. Chelicerae restrainedly strong, with 2 promarginal teeth and 1 retromarginal tooth. Maxillae, labium and sternum elongated. Legs strong and long, usually heavily haired, especially in males. Legs I the strongest, legs III the shortest or as long as legs II. Tibial spines on legs I and II present. The number and size of the tibial spines tend to be reduced. In *O. melanopyga*, 3 pairs of spines on tibia I, whereas in other species 2 or fewer pairs are present. Palpal organs simple, similar in structure to some *Holoplatys* species (Zabka, in preparation) but dorsal apophysis on tibia never present. Lateral apophysis shows specific variability. Tegulum rather oval, embolus long, based on soft, membraneous distal haematodocha. Epigyne in the form of inverted hearth divided by central bridge. Internal structures translucent, insemination ducts of the shape of reversed "U" or "V". Spermathecae pear-shaped, accessory glands long. Female body usually longer, especially abdomen. Male first legs longer and more haried than those in females.

**Relationships.** General similarities to some species of *Holoplatys* (Zabka, in preparation): body shape, genitalia and legs structure shows both genera to be closely allied. The morphology of particular species, especially their cephalothorax proportions and leg spination suggest that the genus probably derived from large, robust spiders showing a tendency to live under bark — at least as facultative inhabitants. A process of specialisation effected a gradual body flattening and reduction of spines on tibiae I and II. Apart from representatives of the related genus *Holoplatys* there are some other species known as "*Breda jovialis* (L.K.)" and "*Menemerus bracteatus* (L.K.)" (both described under wrong generic names) which present some similarities in body shape and epigyne structure; their palpal organs, however, are quite different. As far as I can determine none of the described Australian, South American and African genera of jumping spiders can be regarded as ancestors of *Ocrisiona*. Thus *Ocrisiona* probably originated on the Australian continent and represents one of its many endemic genera.

Similarities of genitalia between many, even unrelated, groups of Salticidae are a good example of convergence. Probably very sophisticated behavioural and also ecological and geographical mechanisms were adequate to provide effective isolation and, in such cases, natural selection did not prefer any large variability of genitalic structure. Such a situation makes identification rather difficult, especially for those who treat genitalia as the only taxonomic character. Therefore other taxonomic characters such as armament of first and second legs, body size and ratios, and colouration are highly recommended.

**Biology.** *Ocrisiona* species can be found mostly under bark of *Eucalyptus*. Single specimens of *O. melancholica* have also been found under *Araucaria* bark (North Queensland) and under lichen on rock surfaces (Lord Howe Island). There is one report from Queensland about *O. leucocomis* being implicated in human envenomation. Local swelling and erythema occurred without any further consequences. Being moderately large spiders some species are probably able to penetrate human skin. The symptoms mentioned could be an individual allergic reaction. In fact, no detailed data about the venom of jumping spiders is available.

**Distribution.** *Ocrisiona* seems to be an endemic

Australian genus. Only single species have expanded their ranges to adjacent areas, possibly introduced by man or dispersed in other ways. *Ocrisiona leucocomis* and *O. melancholica* are mainland species which also occur in Tasmania and Lord Howe Island respectively. *Ocrisiona melanopyga* is reported from Tasmania only. The localities of some species in North Queensland and, especially, in Torres Strait, suggest that representatives of the genus can be expected in New Guinea.

***Ocrisiona leucocomis*** (L. Koch, 1879)
Figs 2A–C, 3A–E, Map 1

*Marptusa leucocomis* L. Koch, 1879: 1096.
*Ocrisiona leucocomis*.—Simon, 1901a: 596, 602, 608, 609.

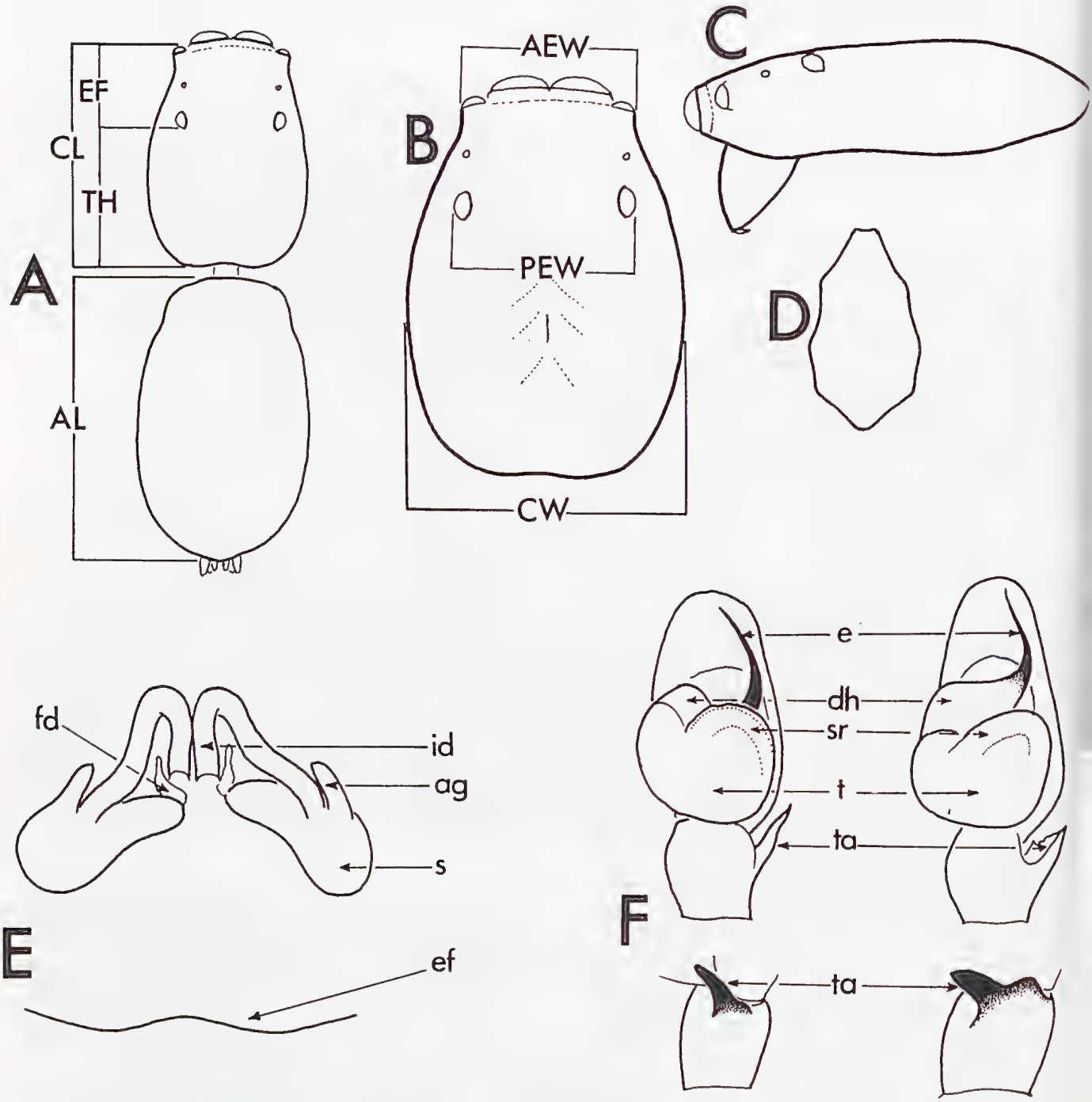



**Fig.1.** General characters of *Ocrisiona*. A: dorsal view: CL — cephalothorax length; AL — abdomen length; EFL — eye field length; TH — thorax. B: cephalothorax: AEW — width of ALE; PEW — width of PLE; CW — cephalothorax width. C: lateral view of cephalothorax. D: sternum. E: internal structures of epigyne: id — insemination duct; fd — fertilisation duct; s — spermatheca; ag — accessory gland. F: palpal organs: e — embolus; dh — distal haematodocha; sr — seminal reservoir; t — tegulum; ta — tibial apophysis.

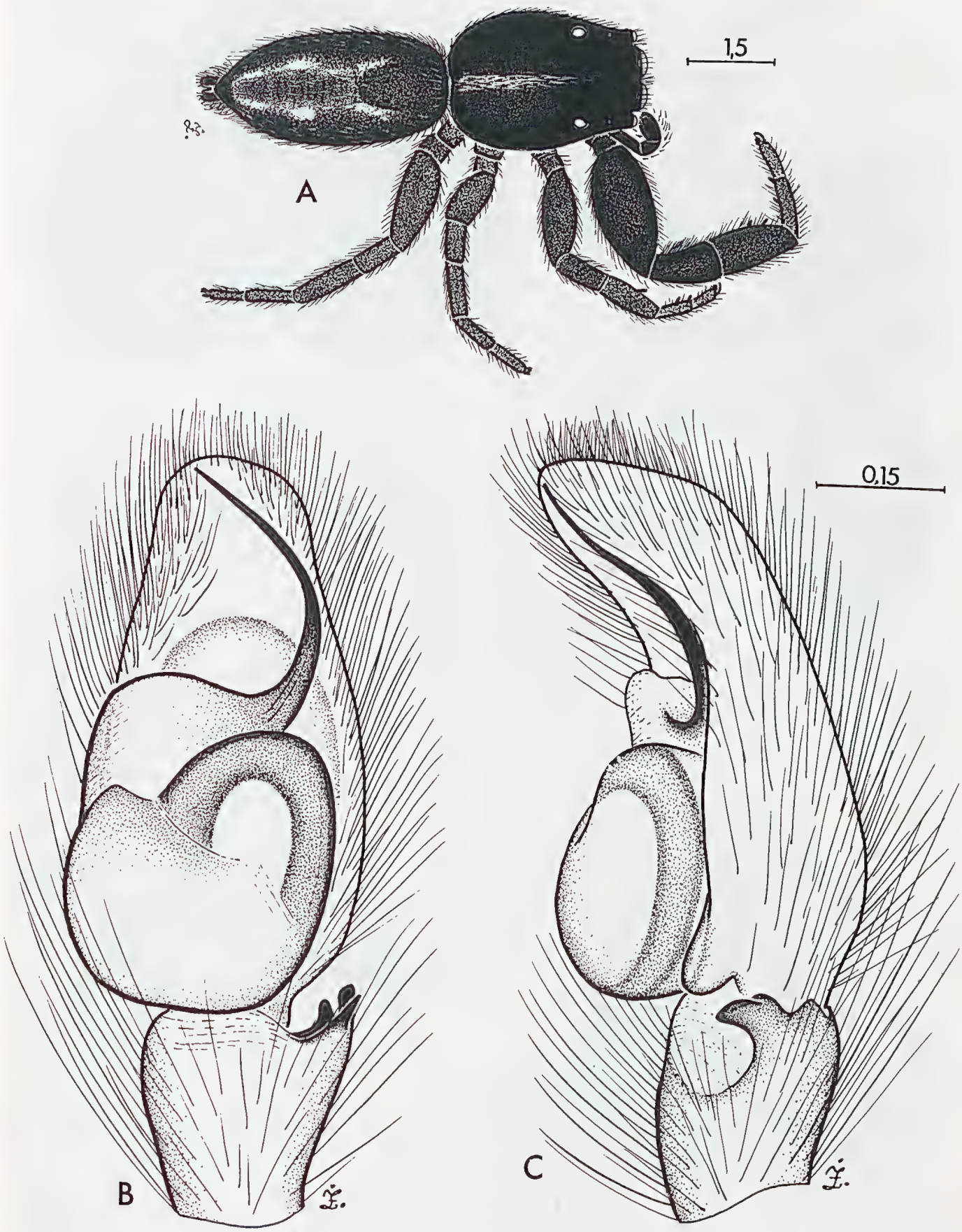



**Fig.2.** Male *Ocrisiona leucocomis*. A — general appearance; B–C — palpal organ (syntype from type locality).

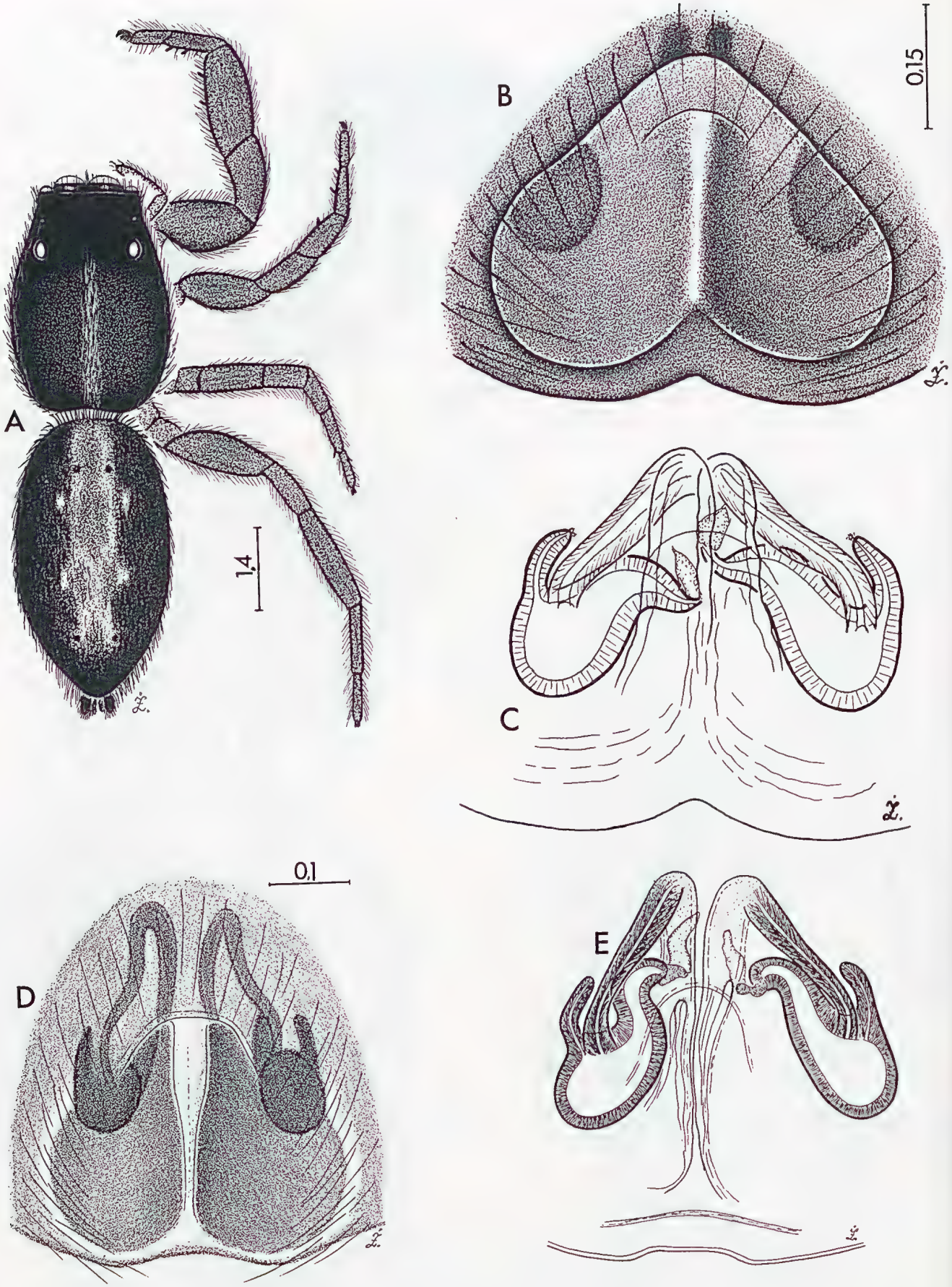



**Fig.3.** Female *Ocrisiona leucocomis*. A — general appearance; B–E — epigyne and its internal structures (A, D–E — syntype from type locality).

**Material examined.** QUEENSLAND: 1 female, Kuranda, Black Mountain, 396 m, edge of wet sclerophyll and rainforest, 19 June 1974, N.C. Coleman, det. M. Gray, AMS KS18868; 1 female, Kuranda area, 1951, J.G. Brooks, AMS KS17741; 2 males, 3 females, 1 juvenile, syntypes, Peak Downs, Sydney, Bowen (Mus. Godeffroy 16523), ZMH; 1 female, Blackdown Tableland, south-west of Rockhampton, 5-6 Oct. 1982, A. Rozefelds, QMB S4608; 1 female, Blackdown Tableland via Dingo, 1-6 Feb. 1981, R. Raven, QMB S458; 1 female, Mount Garnet, 24 Feb. 1972, N.C. Coleman, QMB S4577; 1 male, Kroombit Tops (Upper Dry Creek), 45 km south-west of Calliope, open forest, 9-19 Dec. 1983, V. Davies, J. Gallon, QMB S4569; 2 males, 1 female, 2 juveniles, Muncoonie via Birdsville, campsite, 14 Nov. 1976, QMB S4615; 2 females, 1 juvenile, desert sand plain, R. Raven, QMB S4604; 1 female, Miles, 14 Dec. 1984, J. Gillet, QMB S4562; 2 females, Oakey, Feb. 1979, T. Adams, QMB S4561; 1 male, 1 female, Brisbane, Lake Broadwater, buildings, 1-15 Nov. 1984, V. Wood, QMB S4614, 1 female under bark, 24 Aug. 1984, M. Bennie, QMB S3635; 1 female, Brisbane, Rochedale S.F., beating, 7 Dec. 1979, V. Davies, R. Raven, QMB S4586; 1 female, 10 km south-east of Stanthorpe, 8 May, 1983, A. Rozefelds, QMB S4576. NEW SOUTH WALES: 1 male, Armidale, 1 Jan. 1982, R. Mascord, AMS KS10425; 1 female, Yarramundi, 19 Sept. 1966, R. Mascord, AMS KS18867; 1 female, Tarana, 23 Apr. 1966, R. Mascord, AMS KS18870; 1 male, 1 female, Blue Mountains, Shaw's Creek, 7 Aug. 1968, R. Mascord, AMS KS18869; 1 female, Lindfield, May 1976, A. Doubleday, det. M. Gray, AMS KS18873; 1 male, Botany, 7 Jan. 1975, R. Mascord, AMS KS18874; 1 female, Pambula, "Fernbank", H. Forde, AMS KS18865. WESTERN AUSTRALIA: 1 male, Perth, Museum building, 16 Jan. 1980, K. McNamara, WAMP 88/32; 1 female, Horseshoe Cave near Madura, floor, 13 Feb.-1 Mar. 1970, M. Archer group, WAMP 74/117; 1 female, Madura, Roaches Rest Cave, surface, 27 Dec. 1967, M. Gray, AMS KS18866. TASMANIA: 1 female, Snowy Mountains Range, 457 m, Feb. 1939, C.D. King, TMH J2754. NO LOCALITIES: 2 females, Jan. 1908, Harris, AMS KS17861; 1 female, AMS KS18252.

Map 1. Distribution of *O. leucocomis* (L.K.).

**Diagnosis.** The species can be recognised by the following combination of characters: abdomen with 2 or 3 pairs of light spots along pale mid-dorsal stripe, central stripe of white setae along cephalothorax, length of male embolus and shape of tibial apophysis, curved accessory glands of female epigyne.

*Male* (Fig.2A): cephalothorax almost black with median thoracic stripe of white hairs, less numerous marginal white hairs also present. Abdomen dark grey to black, its anterior part with a poorly visible scutum. Medium longitudinal light stripe with more or less distinct 2 or 3 pairs of lighter spots. Clypeus dark-brown to black with whitish hairs, chelicerae of the same colour with similar hairs basally. Maxillae and labium dark brown to black with lighter tips, sternum brown to black, venter and spinnerets grey brown to black. Legs I of the same colour as body, haired, legs II–IV slightly lighter. Palpal organ (Fig.2B–C) with relatively long embolus, distal haematodocha distinct, tibial apophysis with characteristic protuberances.

*Leg spination:* tI: p1–1, r0–0; mI: p1–1, r1–1; tII: p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions:* CL—2.57–4.29 (3.28); CW—1.84–3.16 (2.32); ratio CW:CL—0.67–0.73 (0.70); EFL—0.85–1.32 (1.05); ratio EFL:CL—0.31–0.33 (0.32); AEW—1.36–1.98 (1.59); PEW—1.37–2.11 (1.66); AL—2.57–5.41 (3.71).

*Female* (Fig. 3A): the body coloured as in male, but specimens usually larger, more robust, legs I relatively shorter. Epigyne (Fig.3B–E) typical in the form, insemination ducts long, accessory glands curved.

*Leg spination:* tI: p1–1, r0–0; mI: p1–1, r1–1; tII: p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions:* CL—4.09–5.41 (4.60); CW—2.87–3.89 (3.23); ration CW:CL—0.68–0.72 (0.69); EFL—1.25–1.58 (1.38); ratio EFL:CL—0.29–0.31 (0.30); AEW–1.91–2.31 (2.09); PEW—1.98–2.51 (2.19); AL—5.28–9.43 (6.54).

In the original description no holotype specimen was designated. The localities "Sydney, Bowen and Peak Downs" were given but the origin of each individual in the syntype series (see above) is unknown.

**Distribution** (Map 1). Widespread species from North Queensland through New South Wales and Tasmania to Western Australia.

### *Ocrisiona melanopyga* Simon, 1901
Fig. 4A–C, Map 2

*Ocrisiona melanopyga* Simon, 1901b: 160.

**Material examined.** TASMANIA: 1 female, Launceston, MNHN 4.736.

**Diagnosis.** Robust spider, cephalothorax and abdomen much wider than in other species, legs I with 3 pairs of tibial spines, dorsal stripe of white hairs on pedipalps, insemination ducts of epigyne broad, especially

proximally.

*Female* (Fig. 4A): cephalothorax robust. Eye field black, thorax brown with white hairs along its median and marginal part. Abdomen dark brown, centrally slightly paler with transverse stripes posteriorly. Whitish hairs present, especially anteriorly and laterally. Spinnerets blackish. Clypeus and chelicerae black brown, the last with single white hairs. Pedipalps orange brown with dorsal longitudinal stripe of white hairs and long lateral fringes. Maxillae and labium black brown with yellow tips, sternum red orange, venter beige. Legs I strong, black brown, others slightly paler. Epigyne (Fig. 4B-C) in the form of triangular depression, insemination ducts broad proximally, distally gradually narrower.

*Leg spination:* tI: p1-1-1, r1-1-1; mI: p1-1, r1-1; tII: p1-1, r1-1; mII: p1-1, r1-1.

*Dimensions:* CL – 5.30; CW – 4.09; ratio CW:CL – 0.81; EFL – 1.58; ratio EFL:CL – 0.30; AEW – 2.44; PEW – 2.57; AL – 5.94.

The original description (Simon, 1901) is based on a male specimen only. A female from the Paris collection has never been described but it has been identified by Simon himself and also its locality suggests it represents *O. melanopyga*. The robust body and spination of tibia I suggest that this species can be the closest to the ancestors of the genus.

**Distribution** (Map 2). The species is known only from Launceston in Tasmania.

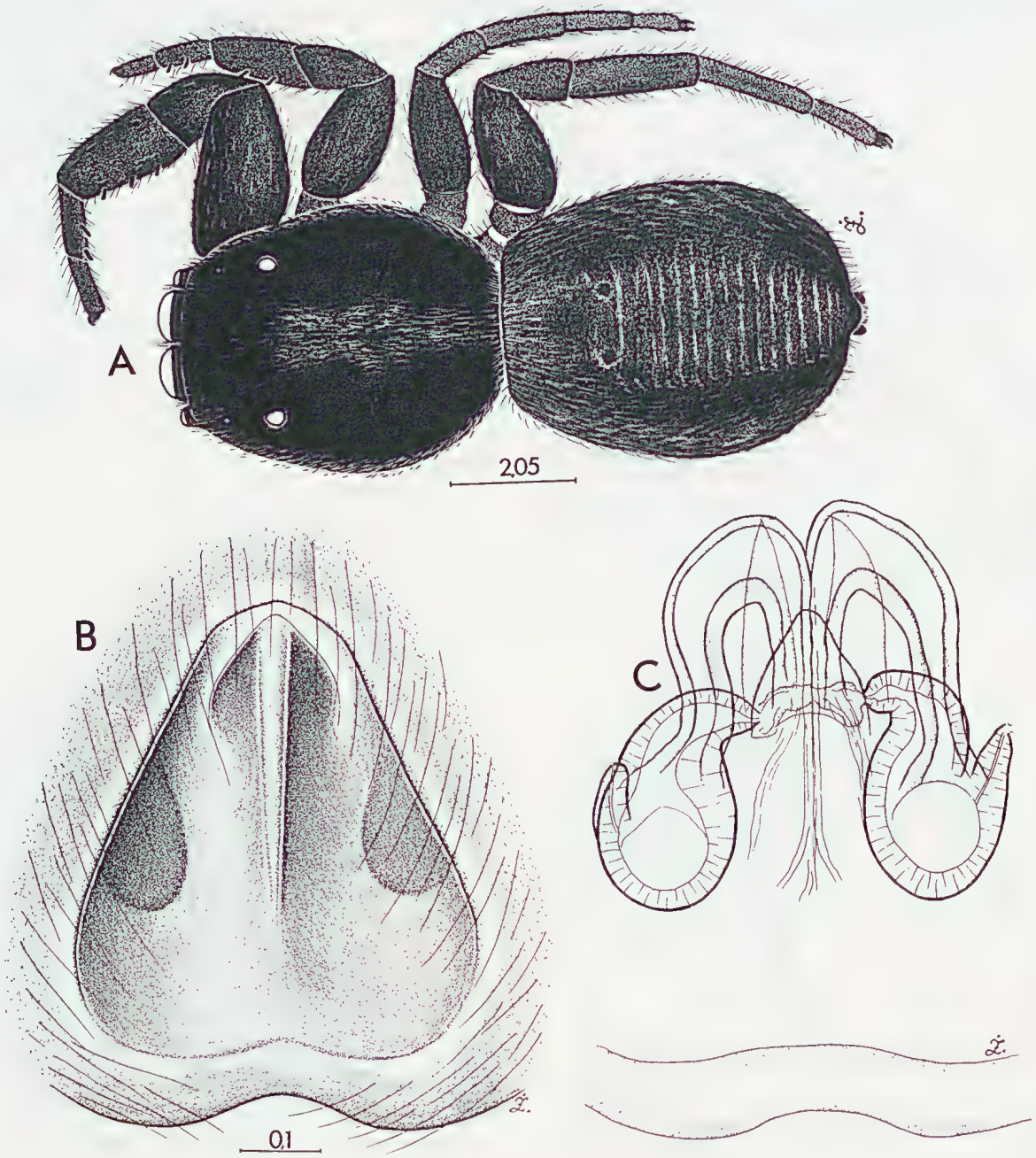



**Fig.4.** Female *Ocrisiona melanopyga*. A — general appearnace; B–C — epigyne and its internal structures (specimen from Launceston).

### *Ocrisiona victoriae* n.sp.

Fig. 5A–C, Map 2

**Material examined.** VICTORIA: Holotype, 1 male, Melbourne, Mar. 1981, D. Hill, QMB S4584.

**Diagnosis.** Abdomen with wide light dorsal stripe, palpal embolus shorter than in other species, accompanied by large distal haematodicha, tibial apophysis with characteristic cusps.

*Male* (Fig. 5A): robust spider. Cephalothorax dark brown with white hairs medially and single ones marginally.

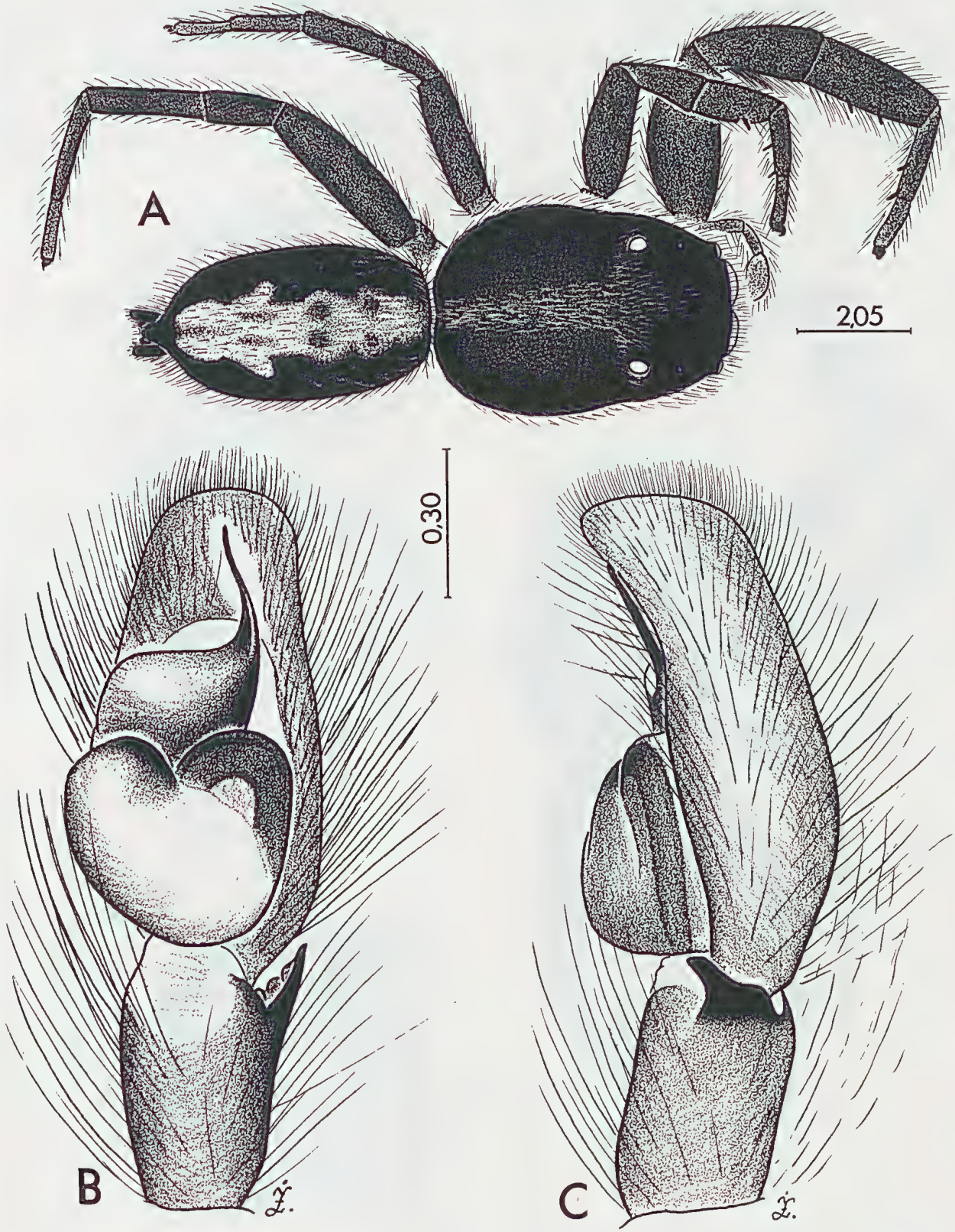



**Fig.5.** Male *Ocrisiona victoriae* n.sp. A — general appearance; B–C — palpal organ.

Abdomen black with light dorsal stripe. Spinnerets black brown. Clypeus and chelicerae black, maxillae dark brown with whitish tips, labium dark brown. Sternum brown, venter beige with 2 longitudinal darker streaks. Legs I dark brown, the others slightly larger. All, but especially first legs, covered with dark and whitish hairs. Palpal organ (Fig. 5B–C) more elongated than in other species, embolus shorter, distal haematodicha larger, tibial apophysis with internal cusps.

*Leg spination:* tI: p1–1, r0–0; mI: p1–1, r1–1; tII: p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions:* CL—4.95; CW—3.49; ratio CW:CL—0.70; EFL—1.52; ratio EFL:CL—0.30; AEW—2.24; PEW—2.37; AL—4.75.

**Distribution** (Map 2). This species is known only from the single Melbourne locality.

### *Ocrisiona parmeliae* n.sp.

Fig. 6A–C, Map 2

**Material examined.** WESTERN AUSTRALIA: HOLOTYPE male, Parmelia, 2 Nov. 1986, A.E. de Jong, WAMP 88/46.

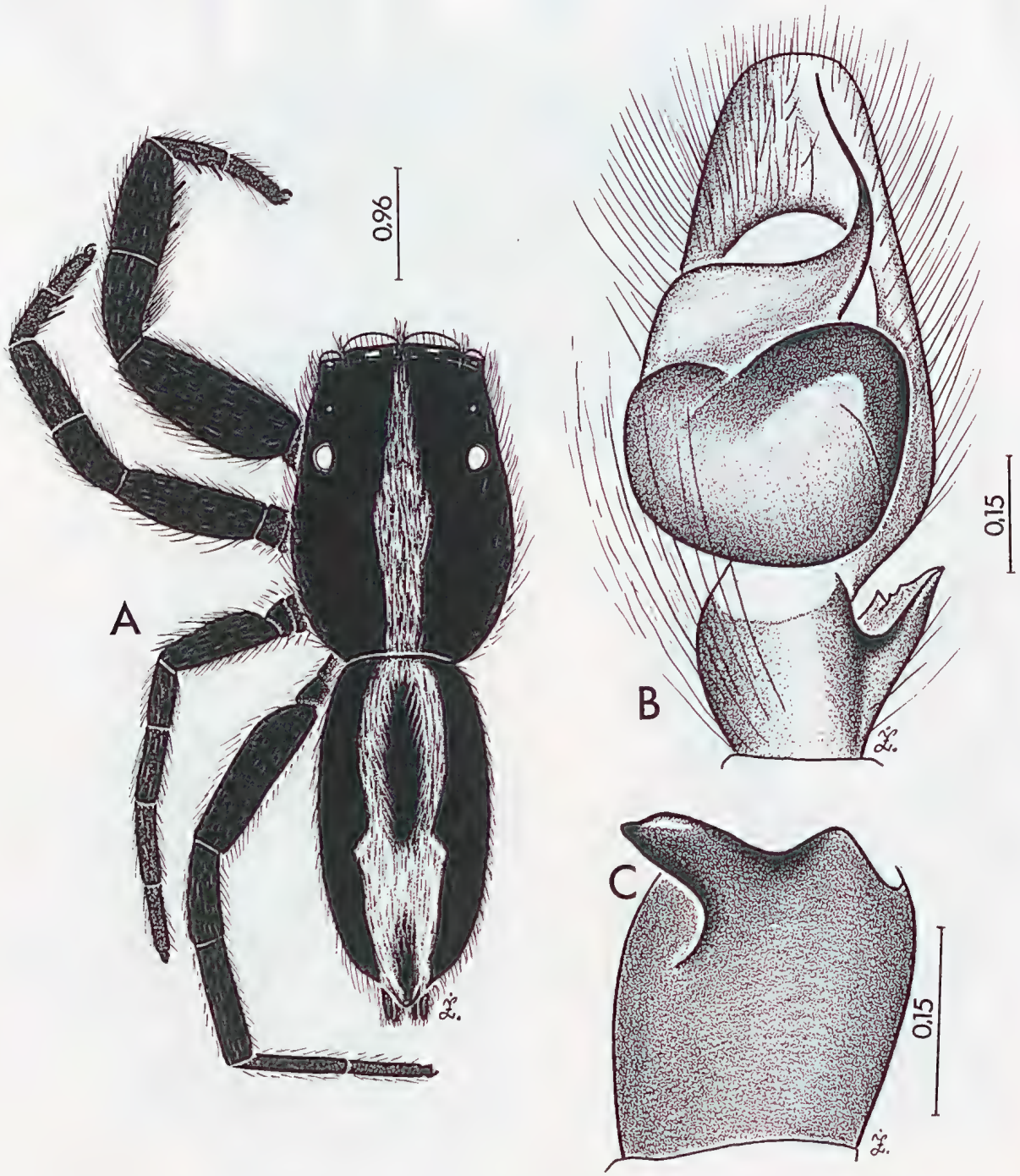



**Fig.6.** Male *Ocrisiona parmeliae* n.sp. A — general appearance; B–C — palpal organ.

**Diagnosis.** The species can be recognised by the following combination of characters: wide mid-dorsal stripe of white hairs along the body. Tibia of palpal organ shorter and wider than in other species, with dorsolateral protrusion, notched on internal edge. Body size relatively small (6mm).

*Male* (Fig. 6A): black spider with characteristic pattern of white hairs. Clypeus with long black hairs. Chelicerae with single whitish scale-like setae, maxillae with lighter tips. Legs I with black hairs, especially on ventral patella and tibia. Other legs less haired. All legs also with white hairs. Palpal organ (Fig. 6B–C) similar to in *O. leucocomis* but tibia shorter and wider and its apophysis of different shape.

*Leg spination:* tI: p1–1, r0–0; mI: p1–1, r1–1; tII: p0–0, r0–0; mII: p1–1, r0–1.

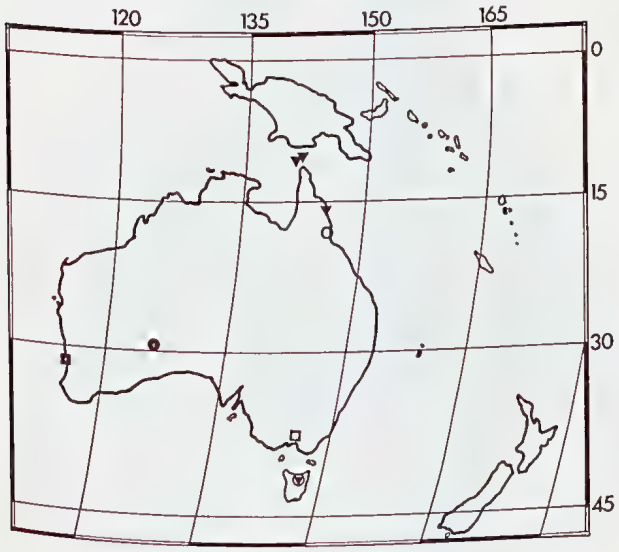
*Dimensions*: CL—2.90; CW—2.04; ratio CW:CL—0.70; EFL—1.05; ratio EFL:CL—0.36; AEW—1.48; PEW—1.55; AL—3.04.

**Distribution** (Map 2). This species is known only from the single Parmelia locality.

***Ocrisiona melancholica*** (L. Koch, 1879)
Figs 7A–E, 8A–C, Map 3

*Marptusa melancholica* L. Koch, 1879: 1113.
*Ocrisiona melancholica*.—Rainbow, 1911: 292.

**Material examined.** QUEENSLAND: 1 female, Leo Creek, under bark of *Araucaria cunninghami*, 15 Aug. 1972, B. Gray, AMS KS13074; 1 female, Kroombit Tops (Upper Kroombit Creek), 45 km south-west of Calliope, open forest, 9-19 Dec. 1983, V. Davies, J. Gallon, QMB S4589; 1 juvenile, rainforest, QMB S4592; 2 females, Gympie, W.W. Frogatt, AMS KS13315; 1 female, Brisbane, Victoria Park, 3 Aug. 1979, N. Cotsell, R. Raven, QMB S4602; 1 female, Lamington National Park, 25 Feb. 1937, H.A. Longman, QMB W702; 1 female, Girraween National Park, 7 Sept. 1983, R.R. Jackson, QMB S4575. NEW SOUTH WALES: 1 juvenile, Brooklana, East Dingo, June 1929, W. Heron, AMS KS18238; 1 female, Yarramundi, 19 Sept. 1965, AMS KS18853; 1 female, Pitt Town, 23 July 1967, C.E. Chadwick, AMS KS18854; 1 female, Mount Coolongatta, 8 Aug. 1966, R. Mascord, AMS KS18852. SOUTH AUSTRALIA: 1 female, Wongawilli, 13 Aug. 1966, R. Mascord, AMS KS18855. LORD HOWE ISLAND: 2 females, AMS KS18856, 1 female Dec. 1923, A. Musgrave, G. Whitby, AMS KS18858, 1 male under lichen on wet rock wall, Feb. 1971, M. Gray; AMS KS18859. The female holotype together with syntypes of *O. leucocomis* from their type locality (ZMH 16523) were examined.




Map 2. Distribution of six species of *Ocrisiona*: *O. eucalypti* (open circle); *O. koahi* (inverted triangle); *O. melanopyga* (inverted triangle in circle); *O. parmeliae* (closed square); *O. victoriae* (open square); *O. yakatunyae* (closed circle).

**Diagnosis.** The species can be distinguished by the following characters: large pale abdominal patches in both sexes, spination of tibiae I and II and genitalia structure.

*Male* (Fig. 7A): cephalothorax brown to black, eye field black, thoracic part with stripe of white hairs, the same hairs also scattered on eye field and marginally. Abdomen grey brown to brown with large light patches. Clypeus brown to black with single long grey hairs. Chelicerae black brown, lighter distally with long white hairs. Maxillae and labium black brown, their tips lighter. Sternum dirty drown, darker marginally, venter grey. Legs black brown proximally, distally lighter. Legs I heavily haired. Palpal organ (Fig. 7B–C) similar to *O. leucocomis* but embolus much shorter, less curved, tibial apophysis of different shape.

*Leg spination:* tI: p0–1, r0–0; mI: p1–1, r1–1; tII: p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions*: CL—4.22; CW—3.03; ratio CW:CL—0.71; EFL—1.26; ratio EFL:CL—0.29; AEW—1.95; PEW—1.98; AL—4.88.

*Female* (Fig. 8A): very similar to male, legs I slightly shorter, abdomen longer. Epigyne (Fig. 9B–E) very similar to that of *O. koahi* n.sp.

Map 3. Distribution of *O. melancholica*.

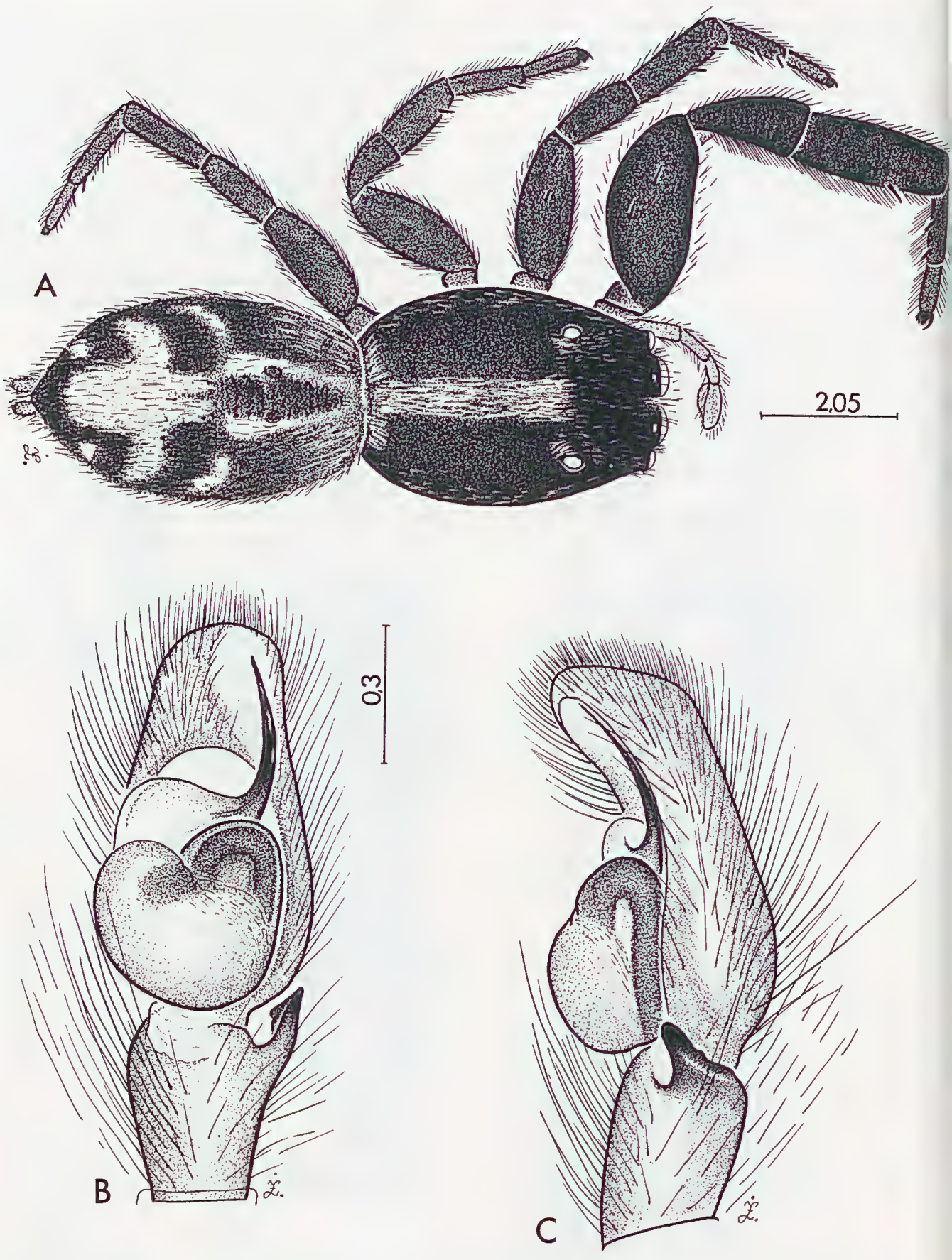



**Fig.7.** Male *Ocrisiona melancholica*. A — general appearance; B–C — palpal organ (specimen from Lord Howe Island).

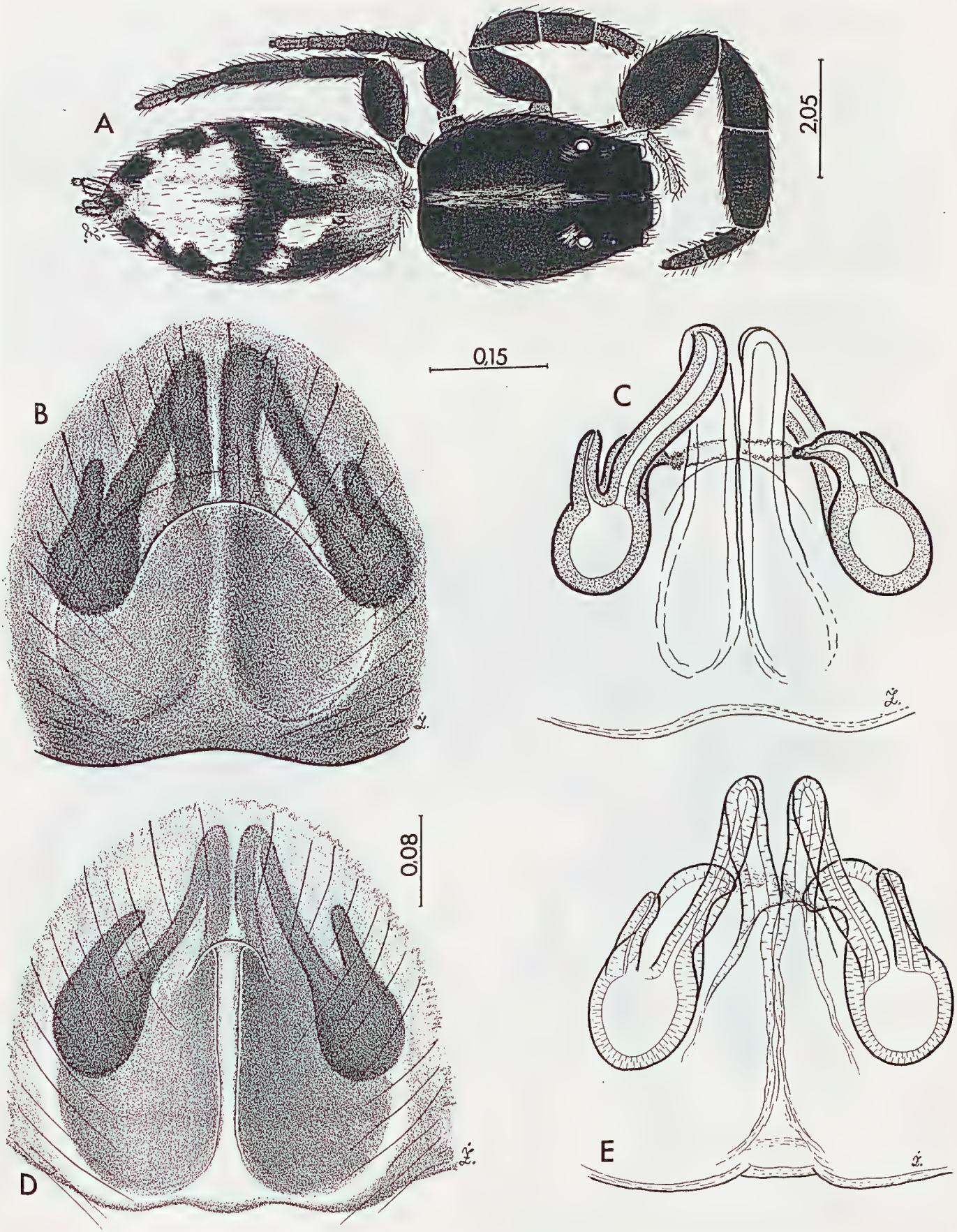



**Fig.8.** Female *Ocrisiona melancholica*. A — general appearance; B–E — epigyne and its internal structures (A–C — specimen from Lord Howe Island; D–E — specimen from Hamburg collection, precise locality unknown, see material studied).

*Leg spination*: tI: p0–1, r0–0; mI: p1–1, r1–1; tII: p0–0, r0–0; mII: p1–1, r1–1.

*Dimensions*: CL—3.50–4.68 (3.96); CW—2.44–3.30 (2.70); ratio CW:CL—0.65–0.70 (0.68); EFL—1.05–1.38 (1.19); ratio EFL:CL—0.28–0.32 (0.30); AEW—1.65–2.05 (1.79); PEW—1.75–2.18 (1.88); AL—4.16–5.48 (5.13).

The type specimen (female), originally described from Bellevue Hill, was not available. One female identified as *O. leucocomis* is found in the Hamburg collection. All specimens used here have been identified on the basis of the original description by Koch.

**Distribution** (Map 3). Widely distributed species, mainly along the coastal part of eastern Australia, including Lord Howe Island.

### *Ocrisiona koahi* n.sp.

Fig. 9A–C, Map 2

**Material examined.** QUEENSLAND: HOLOTYPE female, Koah, 15 Dec. 1971, R. Mascord, AMS KS18837; PARATYPE female, Torres Strait, Horn Island, 23 July 1975, H. Heatwole, E. Cameron, QMB S4571; PARATYPE 1 juvenile, Prince of Wales Island, savannah woodland, under logs, 8 Feb. 1975, QMB S4579.

**Diagnosis.** The species can be recognised by the abdominal pattern and contrasting yellow pedipalps.

*Female* (Fig. 9A): cephalothorax relatively broad, brown, with mid-dorsal stripe of white hairs, cephalic part darker. Abdomen black, covered with numerous black hairs, with characteristic pattern of white setae. Spinnerets

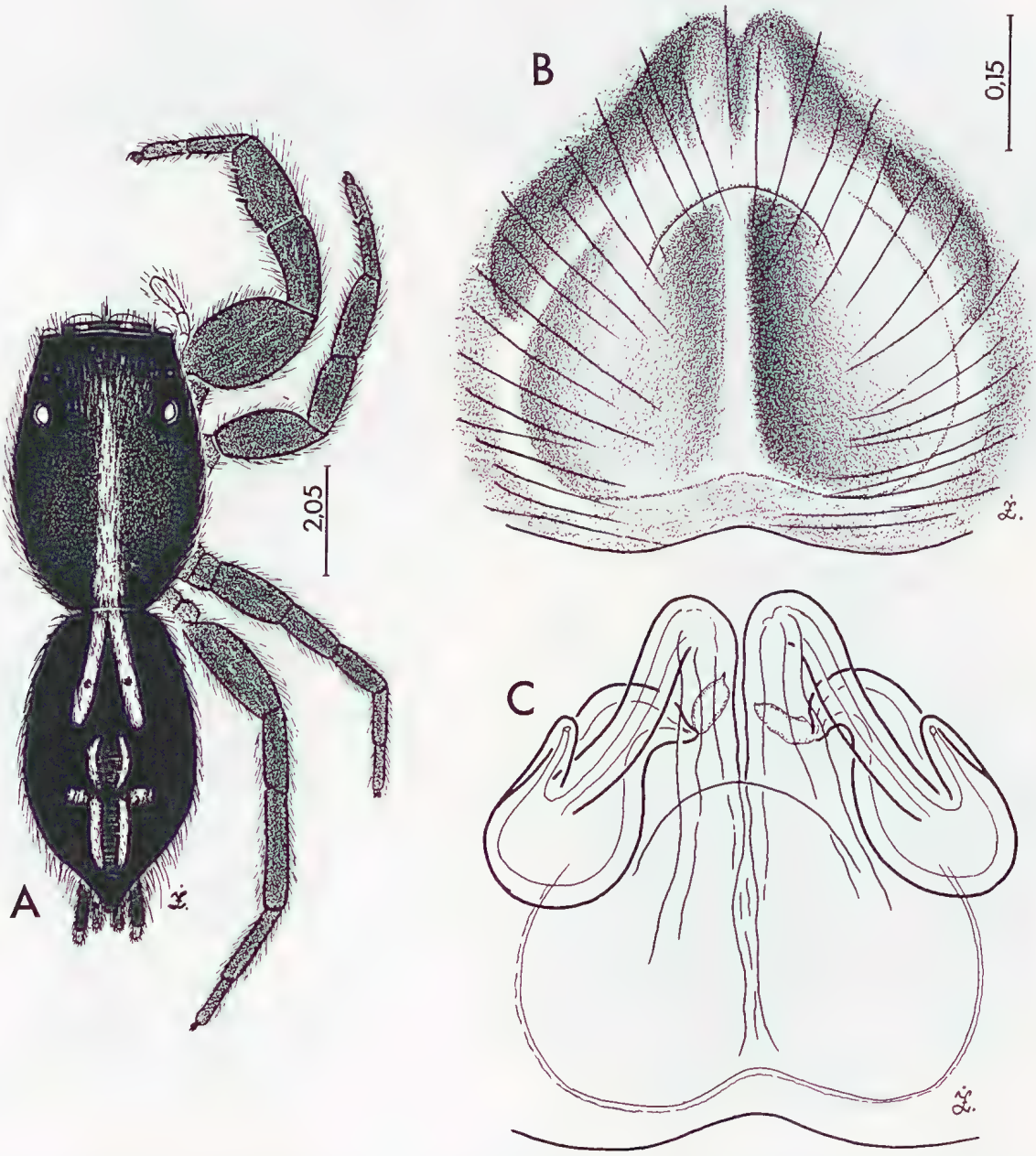



**Fig. 9.** Female *Ocrisiona koahi* n.sp. A — general appearance; B–C — epigyne and its internal structures.

dark brown, rather long. Clypeus black brown with single black hairs. Chelicerae relatively massive, brown. Pedipalps contrasting yellow with long white hairs. Maxillae brown with yellow tips, labium and sternum brown, venter dark grey. Legs brown, lighter distally with brown and shorter scattered white hairs. Epigyne (Fig. 9B–C) similar in structure to *O. leucocomis* and *O. melancholica* but accessory glands shorter and not curved.

*Leg spination*: tI: p1–1, r0–0; mI: p1–1, r1–1; tII: p0–0, r0–0 or p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions*: CL—5.41–5.68 (5.54); CW—3.76–4.29 (4.02); ratio CW:CL—0.69–0.75 (0.72); EFL—1.58–1.84 (1.71); ratio EFL:CL—0.28–0.32 (0.30); AEW—2.57–2.64 (2.60); PEW—2.64–2.74 (2.69); AL—5.47–7.45 (6.46).

**Distribution** (Map 2). Tropical Queensland and Torres Strait.

### *Ocrisiona eucalypti* n.sp.

Fig. 10A–C, Map 2

**Material examined.** QUEENSLAND: HOLOTYPE female, Rosella Plains, 100 Mile Swamp, 7 Nov. 1979, K. McDonald, QMB S3571.

**Diagnosis.** The species can be recognised by the following characters: cephalothorax without light median stripe, with small clusters of white hairs around fovea and behind PLE, spermathecae of epigyne almost parallel to epigastric furrow, insemination ducts slightly shorter than in other species.

*Female* (Fig. 10A): eye field black, thorax dark brown. Around fovea and behind PLE small clusters of white hairs. Abdomen ivory black with pale dorsal stripe, yellowish

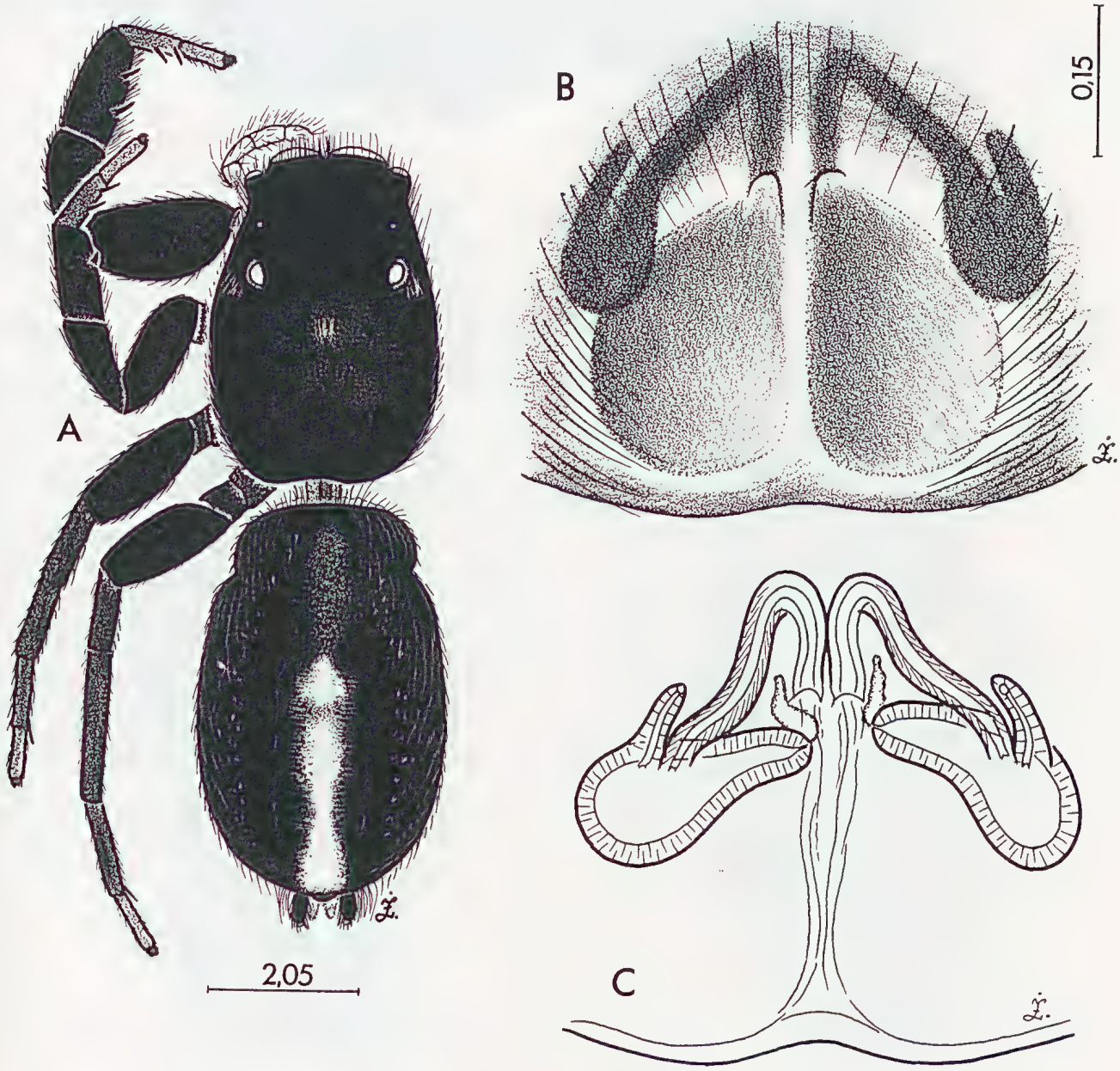



**Fig.10.** Female *Ocrisiona eucalypti* n.sp. A — general appearance; B–C — epigyne and its internal structures.

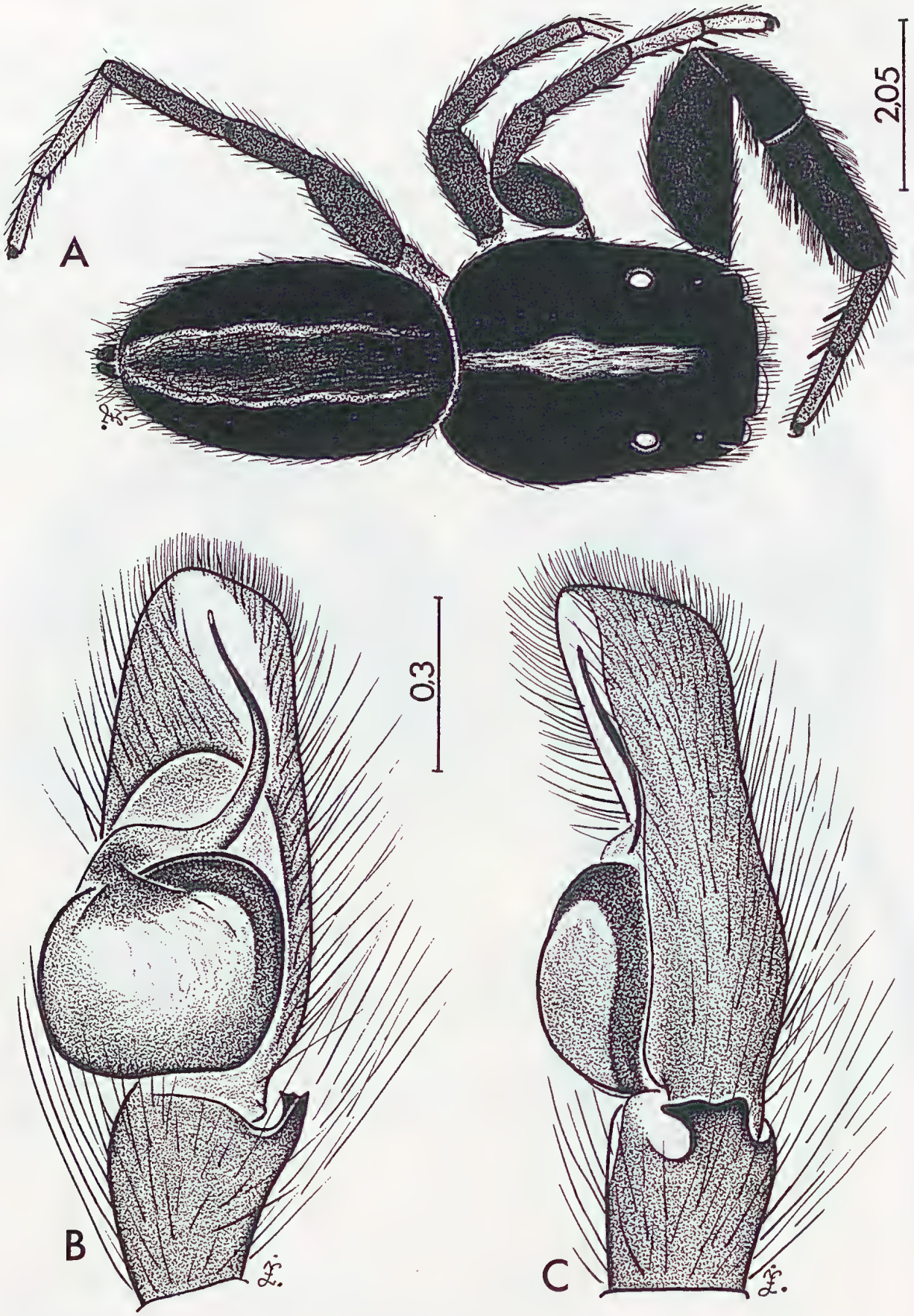



**Fig.11.** Male *Ocrisiona yakatunyae* n.sp. A — general appearance; B–C — palpal organ.

posteriorly. Spinnerets grey and black. Clypeus black with single black hairs, chelicerae black brown with long dark hairs. Pedipalps brown proximally, 3 distal segments contrasting light with yellowish hairs, similar to *O. koahi* n.sp. Maxillae and labium dark brown with light tips, sternum grey brown with darker margin, venter dark grey. Proxima; segments of legs black brown, distal ones gradually lightening posteriorly to orange on tarsi. Legs I heavily haired on ventral patella and tibia. Epigyne (Fig. 10B–C) similar to other species but spermathecae twisted horizontally and insemination ducts shorter.

*Leg spination*: tI: p1–1, r1–0; mI: p1–1, r1–1; tII: p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions*: CL—4.09; CW—2.90; ratio CW:CL—0.70; EFL—1.32; ratio EFL:CL—0.32; AEW—2.11; PEW—2.04; AL—4.95.

**Distribution** (Map 2). This species is only known from the type locality at Rosella Plains, Qld.

### *Ocrisiona yakatunyae* n.sp.

Fig. 11A–C, Map 2

**Material examined.** WESTERN AUSTRALIA: HOLOTYPE male, Yakatunya, 13 Oct. 1987, J. Lark, WAMP 88/40.

**Diagnosis.** The species can be recognised by the following combination of characters: wide cephalothorax, abdominal pattern, the shape of palpal tibial apophysis, relatively small tegulum and long embolus.

*Male* (Fig. 11A): cephalothorax almost black covered with numerous black hairs, with median stripe of white hairs. Abdomen black, hairy, with orange median pattern. Spinnerets black. Clypeus black with similar hairs. Chelicerae black. Maxillae and labium proximally dark brown, distally lighter. Sternum dark brown. Venter brownish grey with 2 longitudinal rows of dirty orange dots. Legs I black brown with metatarsi and tarsi lighter, heavily haired. Other legs slightly lighter with brown and scattered whitish hairs. Palpal organ (Fig. 11B–C) with relatively small tegulum and long embolus. Tibial apophysis with dorsolateral protuberance.

*Leg spination*: tI: p1–1, r0–0; mI: p1–1, r1–1; tII: p0–1, r0–0; mII: p1–1, r1–1.

*Dimensions*: CL—3.70, CW—3.16; ratio CW:CL—0.85; EFL—1.25; ratio EFL:CL—0.33; AEW—1.91; PEW—1.88; AL—3.96.

**Distribution** (Map 2). This species is only known from the type locality at Yakatunya, W.A.

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# *Hickmanoxyomma*, a new genus of cavernicolous harvestmen from Tasmania (Opiliones: Triaenonychidae)

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ABSTRACT. The monotypic genus *Odontonuncia* Hickman, 1958 is redescribed. A new closely related genus, *Hickmanoxyomma*, is described for the type species, *H. cavaticum* (Hickman,1958), and six other species. Two new combinations are established: *H. cavaticum* (*Monoxyomma*) and *H. tasmanicum* (Roewer,1915) (*Monacanthobunus*). One new synonymy is proposed: *Monoxyomma silvaticum* Hickman, 1958 = *H. tasmanicum* (Roewer, 1915). Five new species are described in three species groups: *H. goedei*, *H. clarkei* and *H. eberhardi* (*cavaticum* species group); *H. gibbergunyar* (*tasmanicum* species group); and *H. cristatum* (*cristatum* species group). The distribution of the six cavernicolous and one surface species in *Hickmanoxyomma* and the possible influence of Pleistocene glaciation are discussed. Cavernicolous adaptations, including reductions in lateral branches of claws, are described. Free lateral sclerites are recorded for the first time in the Triaenonychidae and their significance as a family character in the superfamily Travunioidea is discussed.

HUNT, G.S., 1990. *Hickmanoxyomma*, a new genus of cavernicolous harvestmen from Tasmania (Opiliones: Triaenonychidae). Records of the Australian Museum 42(1): 45–68.

Species of *Hickmanoxyomma* n.gen. are the most widely distributed cavernicolous harvestmen in Tasmania (Fig. 1). They occur in almost all karst areas where serious biospeleological studies have occurred (Goede, 1967; Hunt, 1972; Eberhard, 1988; Clarke, 1988). This, together with the varying extent of cave adaptation in different species, means that the group has considerable potential for the study of speciation in isolated cave environments.

## Material and Methods

Type material of all nominal species has been examined and reassessed. The following abbreviations are used to indicate the present location of material examined: AM — Australian Museum, Sydney* (*AM usually denoted simply by the registration number prefix KS), FIS — Forschungsinstitut Senckenberg, Frankfurt am Main, JLH — Dr J.L. Hickman collection, Ferntree, Hobart, QVM — Queen Victoria Museum, Launceston, SAM — South Australian Museum, Adelaide, TMAG — Tasmanian Museum & Art Gallery, Hobart.

Official numbers for caves (e.g. PB3) follow Matthews (1985). Terminology follows Hunt (1985). Tergal areas are abbreviated to TA1, TA2, etc.; coxa of leg I is coxa I, etc.

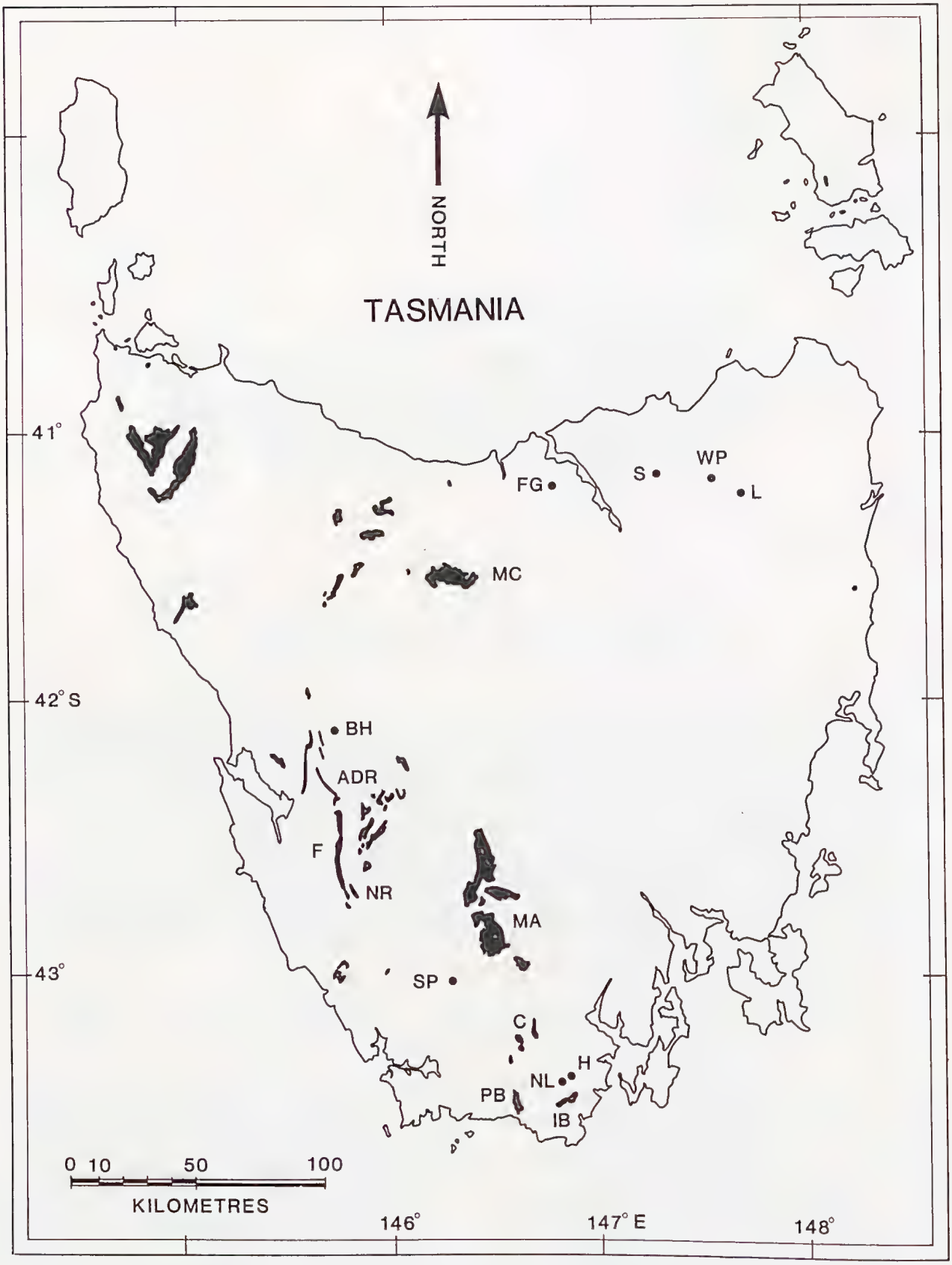


**Fig.1.** Distribution of cavernicolous and epigean *Hickmanoxyomma* spp. in Tasmania. Cave localities: ADR = Andrews River; BH = Bubs Hill; C = Cracroft; F = Franklin River; FG = Flowery Gully; H = Hastings; IB = Ida Bay; MA = Mount Anne; MC = Mole Creek; NL = North Lune; NR = Nicholls Range; PB = Precipitous Bluff; SP = Scotts Peak. Surface localities: L = Lottah; S = Scottsdale; WP = Weldborough Pass. Irregular solids = major karst areas. Adapted from Matthews (1985).

GD = Nei's Standard Genetic Distance. Measurements were made according to Fig. 2 using a Hypad Digitiser; appendage measurements were done retrolaterally along the dorsal profile, articular membranes excluded. Abbreviations are: SA = eyemound spine angle, SH = spine height, IOD = interocular distance, SL = scute length, CW = carapace width, PF = pedipalp femur length, AI & AIV = astragalus I & IV lengths, CI & CIV = calcaneus I & IV lengths, FIV = femur IV length, CSL = cheliceral second segment length.

**Triaenonychidae** Soerensen
**Triaenonychinae** Soerensen

Subfamily taxa in present use have largely been defined by Forster (1954), Briggs (1971b) and Suzuki (1975b). *Hickmanoxyomma* is placed in the Triaenonychinae on the basis of one pair of short side branches on the claws of legs III and IV and the narrow sternum. Two species have lost the side branches as a result of troglomorphic adaptation, a condition also reported for leg III in one cavernicolous *Cyptobunus* Banks in North America (Briggs, 1971b). The Triaenonychinae is also defined on the basis of three pairs of side branches in juveniles, so it is interesting to note that all cavernicolous *Hickmanoxyomma* species, where juveniles are known, either possess two pairs or have lost them completely. The only epigean species has retained the typical number of three pairs.

Although these losses are probable troglomorphies, they point to some plasticity in the form of the tarsal claw. This adds support to the view of Shear (1977) that too much emphasis may have been placed on the form of tarsal claws

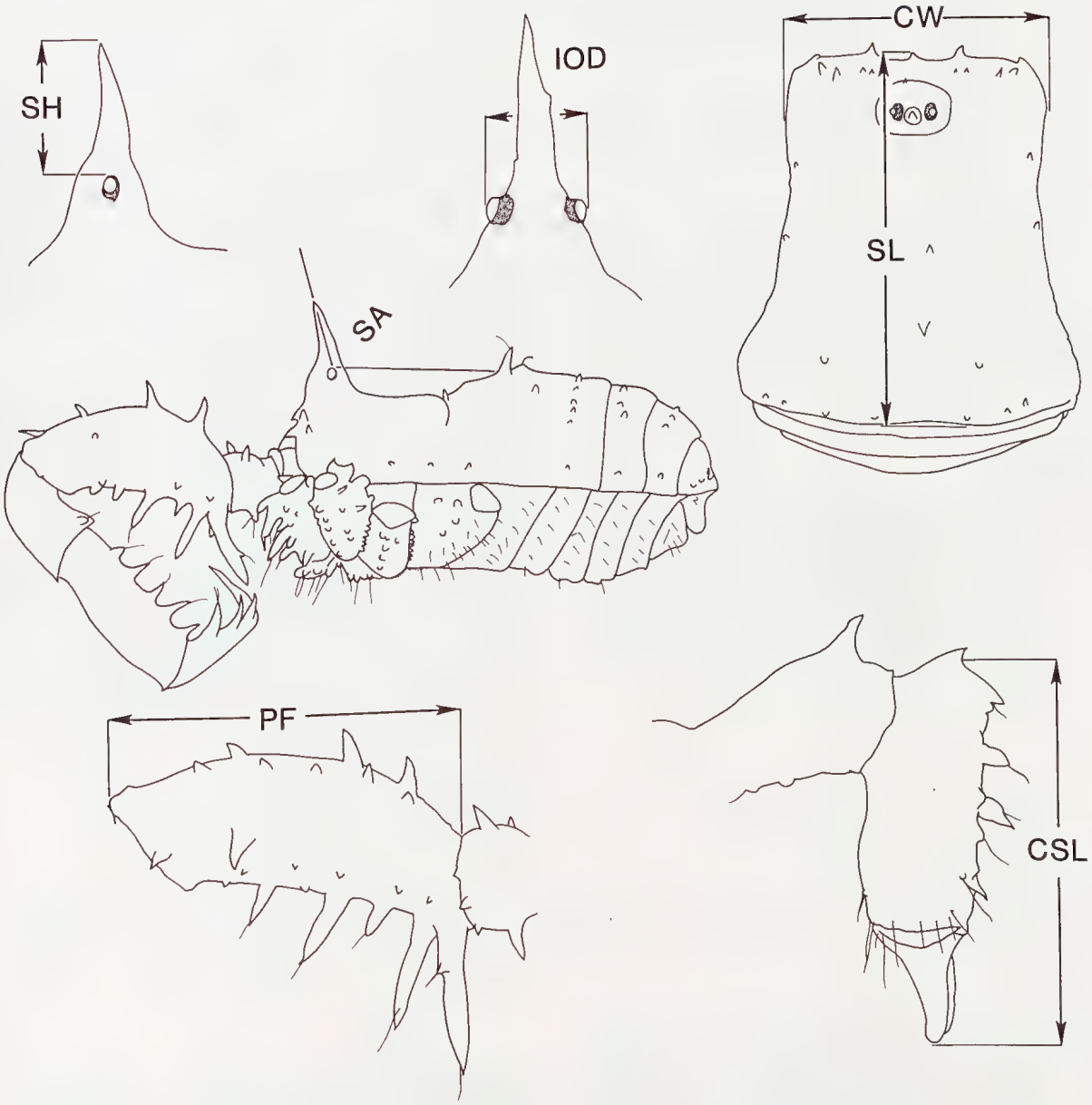


**Fig.2.** Measurement procedures: SH = eyemound spine height; SA = spine angle; IOD = interocular distance; CW = carapace width; SL = scute length; PF = pedipalp femur length; CSL = cheliceral second segment length.

in defining family level taxa in the Travunioidea, including subfamilies in the Triaenonychidae. Indeed, Maury (1988), while placing his new Argentinian troglobitic species, *Picunchenops spelaeus*, in the Triaenonychidae on the basis of penis morphology, deliberately did not assign it to a subfamily — the hind tarsal claws of this species are in the form of a peltonychium, similar to that in the Travuniidae.

Free lateral sclerites are present in several cavernicolous *Hickmanoxyomma* species and is the first record of these structures in the Triaenonychidae. Briggs (1971a) used their presence in certain North American species as part justification for his new family Pentanychidae, while Briggs (1974) and Suzuki (1975a) reported lateral sclerites in North American and Asian Travuniidae.

Normally, lateral sclerites appear to fuse with the sternites. The five free sclerites in *Hickmanoxyomma* (two to three in the mostly epigean Pentanychidae and Travuniidae noted above) may be related to possible reduced sclerotisation due to cave adaptation. Interestingly, however, no lateral sclerites have been described in the highly troglomorphic Travuniidae in Europe or in cavernicolous Triaenonychidae, apart from *Hickmanoxyomma* where their presence or absence is significant in defining species groups.

Free lateral sclerites may be a neotenic reversal, as suggested by Rambla (1980). Alternatively, they may be a persistent character which is plesiomorphic for the superfamily Travunioidea. In either case, their presence in the Triaenonychidae supports the view of Rambla (1980) and Shear (1977) that families in the Travunioidea need reassessment, and add support to Martens' (1986) view, based on penis morphology, that pentanychid taxa belong in the Triaenonychidae.

*Hickmanoxyomma* is very closely related to *Odontonuncia* Hickman and to an undescribed genus from Victoria (including a species from Buchan Caves), both of which also lack a notch in calcaneus I. This group of genera have a penis of similar general form to 3 genera possessing a notch in calcaneus 1, namely *Paranuncia* Roewer, *Holonuncia* Forster and *Equitius* Simon. Together they form a related assemblage inhabiting south-eastern Australia.

## *Odontonuncia* Hickman, 1958

*Odontonuncia* Hickman, 1958: 47.

**Type species.** *Odontonuncia saltuensis* Hickman, 1958 by monotypy.

**Diagnosis.** Eyemound slightly behind anterior margin, armed with a short spine or tubercle. Anterior margin with a few tubercles on each side. TA3 with mesial pair of spines; free lateral sclerites apparently absent (or possibly one present in some specimens). Chelicera without a proximal boss. Pedipalp femur with a proximal compound spine. Calcaneus of leg I without notch. Ventral plate of penis with 3 inferior and 2 superior setae; dorsal plate narrower than glans, short, weakly bifid, with terminal bifurcations not strongly curved and not supporting the glans laterally.

**Redescription.** Eyemound slightly behind anterior margin, armed with a short simple spine or tubercle. Anterior margin below with 5 inter-appendage projections; above with a few small tubercles on each side. Scutal groove distinct mesially; the 5 tergal areas marked by faint tergal grooves and by tubercles or rows of same, mesial pair on TA3 largest. Ninth abdominal tergite fused with anal plate; free lateral sclerites apparently absent. Sternum long and narrow; genital operculum rounded; spiracle abutting coxa IV but only slightly obscured by granules. First segment of chelicera without a proximal boss, with prodistal spine; second segment with upwardly directed proximodorsal swelling. Pedipalp much larger in male; femur with bases of proximoventral trifid spine and proximal retrolateral spine strongly fused to form a compound spine; trifid spine with main shaft and 2 weak accessory denticles; femur spination includes 2 prodistal spines; patella with 2 prodistal spines; tibia and tarsus each with 3 large pro- and retroventral spines; claw movable. Proximal fusion of coxae II & III marked by suture; coxa II with labial process; coxa I with distal proventral compound, but not clavate, spine. Leg femora armed only with small tubercles/granules; calcaneus I without notch, much shorter than astragalus, latter with pseudosegmentation. Male tarsus I with 4 segments, female 3–4; distitarsi I and II with 2 and 3 segments; adult claw of legs III & IV with one pair of short lateral branches (juveniles not seen). Ventral plate of penis with 3 inferior and 2 superior setae on each side, notch shallow; dorsal plate narrower than glans, terminating at level of ventral plate, weakly bifid, with terminal bifurcations not strongly curved and not supporting the glans laterally.

**Comments.** *Odontonuncia* is very closely related to *Hickmanoxyomma* but lacks the synapomorphy of long curved terminations on the dorsal plate which functionally appear to support the glans laterally. *Odontonuncia* apomorphies are the waisted form of the dorsal plate and the form of the proximoventral compound spine on the pedipalp femur.

**Distribution.** North-east Tasmania.

## *Odontonuncia saltuensis* Hickman, 1958
Fig. 3

*Odontonuncia saltuensis* Hickman, 1958: 48–50.

**Type material.** North-east Tasmania: HOLOTYPE male: KS6958, Goulds Country, J.L. Hickman, 16 Aug. 1953. ALLOTYPE female: KS17556, same data.

**Additional material examined.** North-east Tasmania: JLH, Myrtle Creek, north of Mathinna, J.L.

**Fig.3.** *Odontonuncia saltuensis* Hickman. A–D, F–J = Holotype male; E = allotype female. A = body & pedipalp, lateral; B, C = eyemound, lateral & frontal; D, E = pedipalp femur & patella, prolateral, male with posterior enlargement of ventroproximal spines; F = chelicera, retrolateral; G = entire penis; H–J = distal part of penis, ventral, lateral and dorsal. Scale bars: A–G = 1.0 mm; H–J = 0.1 mm.

Hickman, sample 296, 29 May 1973, 14 males, 12 females; JLH, beside creek a few miles south of Myrtle Creek, J.L. Hickman, 15 July 1973, 3 males, 1 female; JLH, Avoca, R. Maubey, 30 Oct. 1972, 1 female.

**Redescription.** MALE. Hickman (1958) gave a detailed non-genitalic description of the species to which can be added: lateral and posterior flanks of eyemound sloping gradually immediately below eyes. TA2 with a larger mesial pair of tubercles than TA1. Spines on TA3 small and blunt. No lateral sclerites unambiguously present in partially distended specimens. Genital operculum wider than long; spiracle barely obscured by tubercles on coxa IV. Chelicera second segment with strong upwardly directed mound on proximodorsal surface. Hickman's "bifid median proximal tooth" is formed from a basal fusion of the proximoventral trifid spine and proximal retrolateral spine of *H. cavaticum*. Accessory denticles on trifid spine weakly developed. Ratio PF:CW 0.90, FIV:CW 1.05, CI:AI 0.18. Lateral branches on claw of legs III & IV small. Tarsal formula:4(2),8–13(3),4,4.

*Genitalia.* Ventral plate with superior setae set very distally; about as long a wide, widest subdistally and narrowing towards base. Notch very shallow, about 0.2 plate length and not reaching distal inferior setae. Lateral plate very narrow basally and broadening distally, not obscuring bases of inferior and distal superior setae. Dorsal plate narrow subdistally and shortly bifurcate. In lateral view glans terminally concave but not deeply cleft.

FEMALE. As in Hickman (1958). Tarsal formula: 3–4(2), 9–11(3),4,4.

**Measurements** (Myrtle Creek sample, n = 3 males, 3 females).

| | SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | | |
| | 5.95-6.51 | 3.92-4.13 | 3.42-3.84 | 2.28-3.02 | 0.51-0.54 | 4.56-5.39 | 0.50-0.54 | 3.98-4.54 | 2.95-3.40 | M |
| | 5.43-5.62 | 3.40-3.68 | 2.73-2.81 | 2.20-2.67 | 0.44-0.46 | 4.43-5.03 | 0.42-0.53 | 3.89-4.12 | 2.45-2.58 | F |
| Mean | | | | | | | | | | |
| | 6.27 | 4.05 | 3.66 | 2.82 | 0.52 | 5.03 | 0.52 | 4.25 | 3.21 | M |
| | 5.52 | 3.50 | 2.76 | 2.51 | 0.45 | 4.75 | 0.46 | 3.98 | 2.52 | F |
| Standard Deviation | | | | | | | | | | |
| | 0.23 | 0.09 | 0.18 | 0.18 | 0.01 | 0.35 | 0.02 | 0.23 | 0.19 | M |
| | 0.08 | 0.12 | 0.03 | 0.16 | 0.01 | 0.25 | 0.05 | 0.10 | 0.05 | F |

**Variation.** The height of the eyemound spine varies from a small granule (Avoca specimen) to slightly higher than that of the holotype.

**Distribution.** North-east Tasmania.

## *Hickmanoxyomma* n.gen.

**Type species.** *Monoxyomma cavaticum* Hickman, 1958 by original designation.

**Diagnosis.** Eyemound slightly behind anterior margin, armed with a long spine. Anterior margin with 2 or more tubercles on each side. TA3 with mesial pair of spines; lateral sclerites present in some species. Chelicera without a proximal boss. Calcaneus of leg I without notch. Ventral plate of penis with 3 inferior and 1 or 2 superior setae; dorsal plate as wide as or wider than glans, long, terminal bifurcations long, strongly curved and support the glans laterally.

**Description.** Eyemound slightly behind anterior margin, armed with a long spine. Anterior margin below with 5 inter-appendage projections; above with 2 or more tubercles on each side. Scutal groove distinct mesially; the 5 tergal areas marked by faint tergal grooves and by tubercles or rows of same, mesial pair on TA3 usually enlarged into spines. Ninth abdominal tergite fused with anal plate; free lateral sclerites present in some species. Sternum long and narrow; genital operculum rounded; spiracle abutting coxa IV but only slightly obscured by granules. First segment of chelicera without a proximal boss, with prodistal spine; second segment with or without upwardly directed proximodorsal swelling. Pedipalp much larger in male; femur with bases of proximoventral trifid spine and proximal retrolateral spine at most weakly fused; trifid spine with main shaft and 2 usually weak accessory denticles; femur spination includes 2 prodistal spines; patella with 2 prodistal spines; tibia with 3 pro- and 5 retroventral spines, tarsus with 3 & 3; claw movable. Proximal fusion of coxae II & III marked by suture; coxa II with labial process; coxa I with distal proventral compound, but not clavate, spine. Leg femora armed only with tubercles/granules; calcaneus I without notch, much shorter than astragalus, latter with pseudosegmentation. Male tarsus I with 4–7 segments, female 3–5; distitarsi I and II with 2 and 3–4 segments; adult claw of legs III & IV with one pair of short lateral branches or branches lacking; juveniles with 2 pairs of lateral branches or lacking. Ventral plate of penis with 3 inferior and 1–2 superior setae on each side, notch shallow; dorsal plate as wide or wider than glans, terminating immediately below terminal expansion of glans, strongly bifid, with terminal bifurcations strongly curved ventrad and supporting the glans laterally.

**Species groups.** Rather than describing formal subgenera, three species groups are defined, namely the *cavaticum*, *tasmanicum* and *cristatum* species groups. Taxonomic treatment follows this order.

**Comments.** *Hickmanoxyomma* is very closely related to *Odontonuncia* and to an undescribed genus from Victoria which includes cavernicoles. It differs from both in two apomorphies: a long spine on the eyemound and long, curved terminal bifurcations to the penis dorsal plate which functionally appear to support the glans laterally. The Victorian genus has a characteristically broad and flattened glans (Hunt, in preparation).

*Monoxyomma* Pocock and *Monacanthobunus* Roewer in which the two described species of *Hickmanoxyomma* were formerly placed are junior synonyms of *Equitius* and

are not available (Hunt, 1985).

**Etymology.** The generic name acknowledges the great contribution of Professor V.V. Hickman to the study of Tasmanian Opiliones, and retains the "*oxyomma*" ("spined eye") fragment of *Monoxyomma* in which Hickman originally placed the type species. Gender is neuter.

**Distribution.** Tasmania.

## Key to Species of *Hickmanoxyomma*

1. Calcaneus of leg 1 greater than 0.4 astragalus length, penis with broad crest-like termination ..... *H. cristatum* n.sp.

—— Calcaneus less than 0.4 astragalus length, penis without broad crest-like termination ..... 2

2. Calcaneus usually less than 0.24 astragalus length, ventral plate of penis widest basally and with 1 superior seta ..... 3

—— Calcaneus usually greater than 0.24 astragalus length, ventral plate of penis widest subdistally and with 2 superior setae ..... 4

3. Mesial pair of tubercles on posterior margin of dorsal scute and on free tergites strong and rounded ..... *H. tasmanicum* (Roewer), n.comb.

—— Posterior margin of scute and free tergites with only small tubercles or granules ..... *H. gibbergunyar* n.sp.

4. Mesial spines on TA3 reduced to small tubercles, lateral prongs on the claws legs III and IV lacking ..... *H. eberhardi* n.sp.

—— Mesial spines of TA3 quite large, lateral claw prongs present ..... 5

5. Eyemound sloping steeply below eyes, mesial spines on anterior margin quite strong, distal 2 pairs of inferior setae inserted at subequal level on ventral plate of penis ..... *H. goedei* n.sp.

—— Eyemound sloping gradually below eyes, mesial spines on anterior margin weak, distal 2 pairs of inferior setae inserted at different levels on ventral plate of penis ..... 6

6. Ventral plate of penis much longer than wide, its notch depth about 0.3 plate length ..... *H. clarkei* n.sp.

—— Ventral plate of penis about as long as wide, its notch depth about 0.5 plate length ..... *H. cavaticum* (Hickman) n.comb.

### *cavaticum* species group

Four species, southern Tasmania, cavernicolous. Ventral plate widest subdistally, 2 superior setae; 5 free lateral sclerites; penis lateral plate broad basally; end of glans deeply cleft in lateral view; chelicera second segment without strong upwardly directed proximodorsal swelling; SA usually greater than 65 deg.; CI:AI usually greater than 0.23 less than 0.40.

**Fig.4.** *Hickmanoxyomma cavaticum* (Hickman). A–C, F–G, I, K = Holotype male; H, J = allotype female. A = body & pedipalp, lateral; B, C = eyemound, lateral and frontal (Ida Bay population); D, E = eyemound, lateral and frontal (male, Hastings population); F = body, dorsal; G = coxosternal region, left side; H = posterior of abdomen showing lateral sclerites (solid); I = chelicera, retrolateral; J, K = pedipalp femur & patella, prolateral, male with posterior enlargement of ventroproximal spines. Scale bars = 1.0 mm

### *Hickmanoxyomma cavaticum*
(Hickman, 1958), n.comb.

Figs 4,5

*Monoxyomma cavaticum* Hickman, 1958: 66–68.

**Type material.** South-east Tasmania: HOLOTYPE male, AM KS6924, Ida Bay Caves, V.V. Hickman, 22 Nov. 1939. ALLOTYPE female, AM KS17864, same data.

**Additional material examined.** South-east Tasmania, Ida Bay, 43°30'S, 146°50'E: Ida Bay Caves (probably Mystery Creek Cave): TMAG, J2858, same data as types, 2 males, 2 females, 2 immature; TMAG, J2859, D.M. Alcock, 12 June 1949, 2 females, 3 immature; TMAG, A. Goede, 22 Dec. 1964, 1 male, 1 female; SAM, A.M. Lea, no date, 1 female. Mystery Creek (Entrance) Cave (IB10): KS20061, A.M. Richards, 10 Nov. 1966, 3 males, 3 females; KS20062, A. Goede, 27 Oct. 1967, 1 male, 2 females; KS20095, A. Goede, 27 Oct. 1967, 1 immature; KS20063, A. Goede, 25 July 1971, 1 female; KS20064, A. Goede, 29 June 1974, 1 female; KS20026, same data, 1 male, 6 females; KS20027, same data, 1 male; KS20065, T. Goede, 15 Nov. 1975, 4 immature; KS20066, A. Goede, 29 Feb. 1976, 1 immature; KS20092, same data, 4 females; KS20106, S. Eberhard, 20 Jan. 1985, 1 female; KS20096, S. Eberhard, 11 Nov. 1986, 1 immature. Exit Cave: KS20067, A. Goede, 2 Mar. 1967, 1 female; KS20068, A. Goede, 27 Feb. 1968, 1 female; KS20069, A. Goede, 3 Nov. 1968, 1 female; KS20070, A. Goede, 3 Nov. 1969, 1 male; KS20071, A. Goede, 23 Mar. 1969, immature; KS20072, Kellers Squeeze, A. Goede, 29 Mar. 1969, 1 male, 1 female; SAM, BS1844, E. Hamilton-Smith, 24 May 1969, 1 male; KS20073, A. Goede, 22 Nov. 1970, 1 male, immature; KS20074, A. Goede, 25 July 1971, 1 male, 1 female; KS20021, Colonnades Chamber, W. Lehmann, 21 Apr. 1971, 1 male; KS20075, A. Goede, 5 Nov. 1972, 1 male, 1 female, immature; KS20076, N. Poulter, 22 Jan. 1973, 1 immature; KS19764, A. Goede, 19 Aug. 1974, 2 males, 1 females; KS20077, A. Goede, 15 Jan. 1975, 2 males; KS20078, in talus, dark zone, A. Goede, 19 May 1974, 1 male; KS20079, A. Goede, 21 Dec. 1974, 1 male, 4 females; KS20093, A. Goede, 1976, 1 male, 1 female; KS20094, Kellars Squeeze, Southern Passage end, A. Clarke, 31 Oct. 1987, 1 male. Loons Cave: KS20097, A. Goede, 13 Jan. 1968, 1 immature; KS20098, A. Goede, 18 Jan. 1969, 2 females. March Fly Pot Cave (IB46): KS20099, A. Clarke & N. Poulter, 23 Jan. 1988, 1 female, 1 immature. Little Grunt Cave (IB23): KS20100, S. Eberhard, 1 Dec. 1984, 1 male. Cyclops Cave (IB57): KS20101, S. Eberhard, 26 Oct. 1985, 1 immature. Hobbit Hole Cave (IB15): KS10102, S. Eberhard, Apr. 1984, Arthurs Folly Cave, KS20103, 300-400m from entrance, S. Eberhard, 21 Nov. 1986, 1 male. KS20146, Revelation Cave (IB1), A. Clarke, 24 Mar. 1989, 1 male; Cave IB97: KS20104, A. Clarke, 21 June 1987, 1 female. Unnamed cave, KS20105, S. Eberhard, 7 Feb. 1986, immature.

Hastings Caves, 43°23'S, 146°51'E: King George V Cave: SAM BS0440, E. Hamilton-Smith, 14 Nov. 1963, 1 male; KS20107, A. and T. Goede, 13 Mar. 1968, 1 male; KS20108, T. Goede, 5 Oct. 1968, 1 male; KS20030, twilight zone, T. Goede, 8 Oct. 1968, 1 male; KS20109, A. Goede, 17 Nov. 1968, immature; KS20110, A. and T. Goede, 24 Mar. 1969, immature; KS20111, same data, 1 male, 1 female; KS20112, T Goede, 17 July 1971, 1 female, 1 immature; KS20028, T. Goede, 21 Oct. 1971, 1 male; KS20029, same data, 2 immature; KS20113, T. Goede, 28 Nov. 1971, 3 immature; KS20114, A. Goede, 8 Jan. 1973, 1 male, 4 females, 3 immature; KS20115, A. Goede, 30 June 1974, 3 males, 2 females; KS20116, T. Goede, 2 Nov. 1975, 2 females; KS20117, A. Goede, 28 Feb. 1976, immature; KS20118, same data, 4 males, 3 females; KS20119, A. and T. Goede, 20 Dec. 1976, 2 females; KS20120, S. Eberhard, 16 Dec. 1984. Trafalgar Cave: KS20121, S. Eberhard, 17 June 1984, 1 immature. Waterloo Swallett Cave: TMAG, R. Eberhard, 31 May 1980, 1 female. Surface collection, side road near King Geoge V Cave, under logs: KS20122, T. Goede, 28 Nov. 1971, 1 male, 1 immature.

North Lune karst area, 43°24'S, 146°50'E: Spiders Den Cave (NL3): KS20123, A. Clarke, 5 Feb. 1988, 1 female.

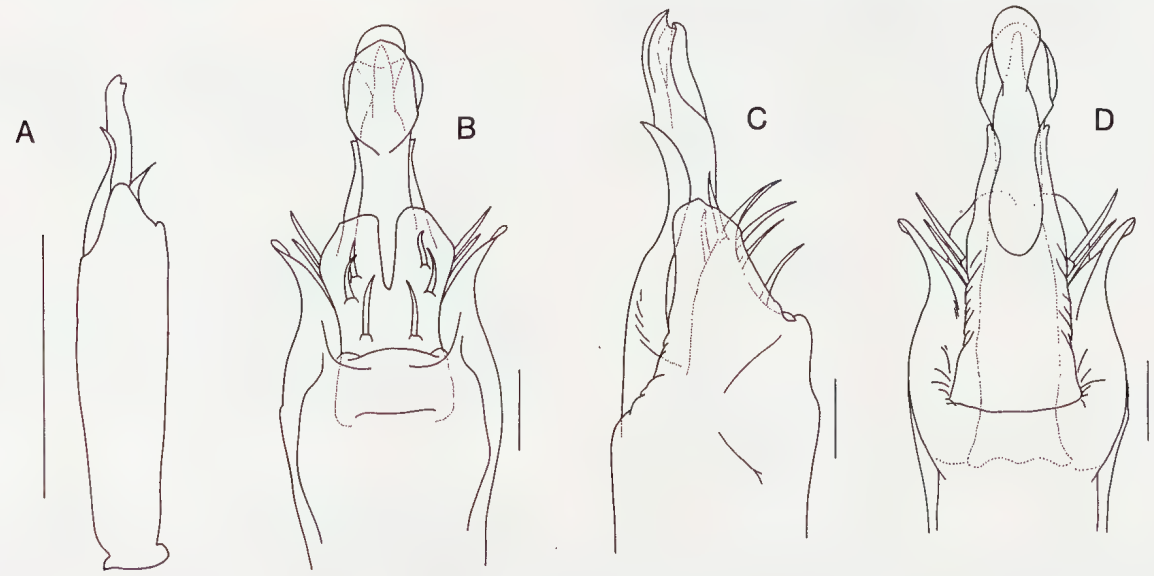


**Fig.5.** *Hickmanoxyomma cavaticum* (Hickman). Holotype penis: A = entire; B-D = distal part, ventral, lateral and dorsal. Scale bars: A = 1.0 mm; B-D = 0.15 mm.

**Diagnosis.** Lateral flanks of eyemound sloping gradually immediately below eyes; genital operculum longer than wide; 4–5 retroventral spines (size order 1,3,4,2,5); calcaneus I about 0.30–0.35 astragalus; ventral plate about as long as wide, notch deep, about 0.5 plate length and reaching beyond distal inferior setae. Lateral plate long, obscuring all or virtually all of proximal superior seta.

**Redescription.** MALE. *Body*. Dorsal colour yellow-brown; pigmentation pattern as figured, faint. Eyemound rising just behind anterior margin; spine suberect, SA about 70°, SH about 1.5 IOD; lateral flanks sloping gradually immediately below eyes. Anterior margin with 2–3 tubercles on each side. TA3 with pair of gracile suberect spines; TA1 with pair small tubercles; TA2 with pair of small granules or lacking, TA4 with more widely spaced pair of tubercles; distribution of other granules as figured. Five lateral sclerites easily seen in distended specimens. Coxosternal region as figured; genital operculum longer than wide; spiracle barely obscured by tubercles on coxa IV.

*Chelicerae*. Prodistal spine on first segment moderately large; second segment without strong upwardly directed mound on proximodorsal surface, dorsal surface with strong proximal spine and another towards the middle.

*Pedipalps*. Gracile; ratio PF:CW 0.93. Femur with row of 3 mediodorsal spines (size order 1,2,3), 4 smaller prodorsal spines, and 4-5 retroventral spines (size order 1,3,4,2,5). Accessory denticles on proximoventral trifid spine weakly developed. Trifid spine and proximal retroventral spine barely joined at base. Tibia with 5 retroventral spines.

*Legs*. Ratio FIV:CW 2.84; calcaneus long, ratio CI:AI 0.35. Lateral branches on claw of legs III & IV small; juveniles with 2 pairs of branches. Tarsal formula: 6–7(2), 18–22,4,4.

*Genitalia*. Ventral plate with 2 superior setae on each side, about as long as wide, widest subdistally and narrowing towards base. Notch deep, about 0.5 plate length and reaching beyond distal inferior setae. Lateral plate broad basally, obscuring all setal bases on ventral plate, and long, obscuring all or virtually all of proximal superior seta. Glans terminally cleft in lateral view.

FEMALE. Similar to male except: body smaller, pedipalps more gracile and relatively shorter, trifid spine more slender, its proximal accessory denticle weaker. Tarsal formula:4–5(2),16–21(3),4,4.

**Measurements** (Exit Cave sample, n = 6 males, 6 females).

| | SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | | |
| | 4.78-5.52 | 3.33-3.81 | 2.93-3.70 | 4.54-5.14 | 1.61-1.78 | 10.28-12.01 | 1.49-1.70 | 9.63-10.51 | 2.47-3.02 | M |
| | 4.15-5.25 | 2.93-3.35 | 2.51-2.78 | 4.39-4.62 | 1.51-1.77 | 9.94-11.59 | 1.35-1.74 | 9.21-9.76 | 2.19-2.52 | F |
| Mean | | | | | | | | | | |
| | 5.09 | 3.49 | 3.24 | 4.87 | 1.69 | 11.10 | 1.63 | 9.91 | 2.64 | M |
| | 4.76 | 3.14 | 2.64 | 4.55 | 1.62 | 10.59 | 1.52 | 9.53 | 2.41 | F |
| Standard Deviation | | | | | | | | | | |
| | 0.26 | 0.17 | 0.27 | 0.21 | 0.06 | 0.52 | 0.08 | 0.31 | 0.15 | M |
| | 0.36 | 0.16 | 0.09 | 0.13 | 0.08 | 0.54 | 0.13 | 0.19 | 0.11 | F |

**Variation.** The Ida Bay and Hastings populations appear to be very similar morphologically except that the latter tends to have a steeper anterior slope and more convex posterior slope to the eyemound (Fig. 4D), FIV:CW 2.73 and CI:AI only 0.28. Tarsal formula: males 6–7(2),18–20(3),4,4; females 4–6(2),16–17(3),4,4. Electrophoretically, there are one fixed and two frequency differences in 13 enzymes assessed, GD = 0.167 (n = 4 & 5 respectively) (D. Coglan, personal communication). The North Lune sample (n = 1) shows two fixed differences from both Hastings and Ida Bay, GD = 0.192 and 0.275 respectively. The results suggest the three populations may well be reproductively isolated. Means for the Hastings population sample (n = 6 males, 5 females):

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| 5.00 | 3.37 | 3.18 | 4.85 | 1.37 | 10.36 | 1.32 | 9.20 | 2.61 | M |
| 4.54 | 2.97 | 2.51 | 4.38 | 1.25 | 9.63 | 1.15 | 8.55 | 2.26 | F |

**Comments.** *H. cavaticum* appears to be very closely related to *H. goedei* and *H. clarkei* but is more troglomorphic. Further electrophoretic work should clarify these relationships and the status of the populations currently regarded as *H. cavaticum*.

**Natural history.** The collection of a teneral adult and juvenile under logs over 100 m from the nearest known cave suggests that the species is capable of moving from cave to cave across the surface. The fact that young specimens were collected suggests that the species may sometimes breed in non-cave habitats or may disperse in the juvenile stage.

**Distribution.** South-east Tasmania: Hastings-Ida Bay karst areas.

### *Hickmanoxyomma goedei* n.sp.

Fig. 6

**Type material.** South Tasmania, Scotts Peak, near Lake Pedder, 43°03'S, 146°18'E. HOLOTYPE male: KS19749, Huon Cave (SP 1,2), A. and T. Goede, 23 Mar. 1974. PARATYPES, KS19765, same data, 1 female; KS19748, same data, 2 males, 2 immature; KS19747, same cave, S. Eberhard, 29 Oct. 1988, 1 male.

**Additional material examined.** South-west Tasmania, Nicholls Range, 42°40'S, 145°50'E: KS20023, cave, in twilight zone, S. Eberhard, 19 Feb. 1987, 1 male; KS20024, same data, 2 females. Bill Nielson (Rotuli) Cave (NR1): KS20060, in dark and twilight zone, S. Eberhard, 19 Feb. 1987, 1 male; KS20025, same data, 4 females.

**Diagnosis.** Lateral flanks of eyemound sloping steeply immediately below eyes. Anterior margin with 2 tubercles on each side, mesial pair close to eyemound and large; TA2 lacking granules; genital operculum longer than wide; dorsal surface of cheliceral second segment with 2 spines towards middle; pedipalp femur with 4–5 retroventral spines

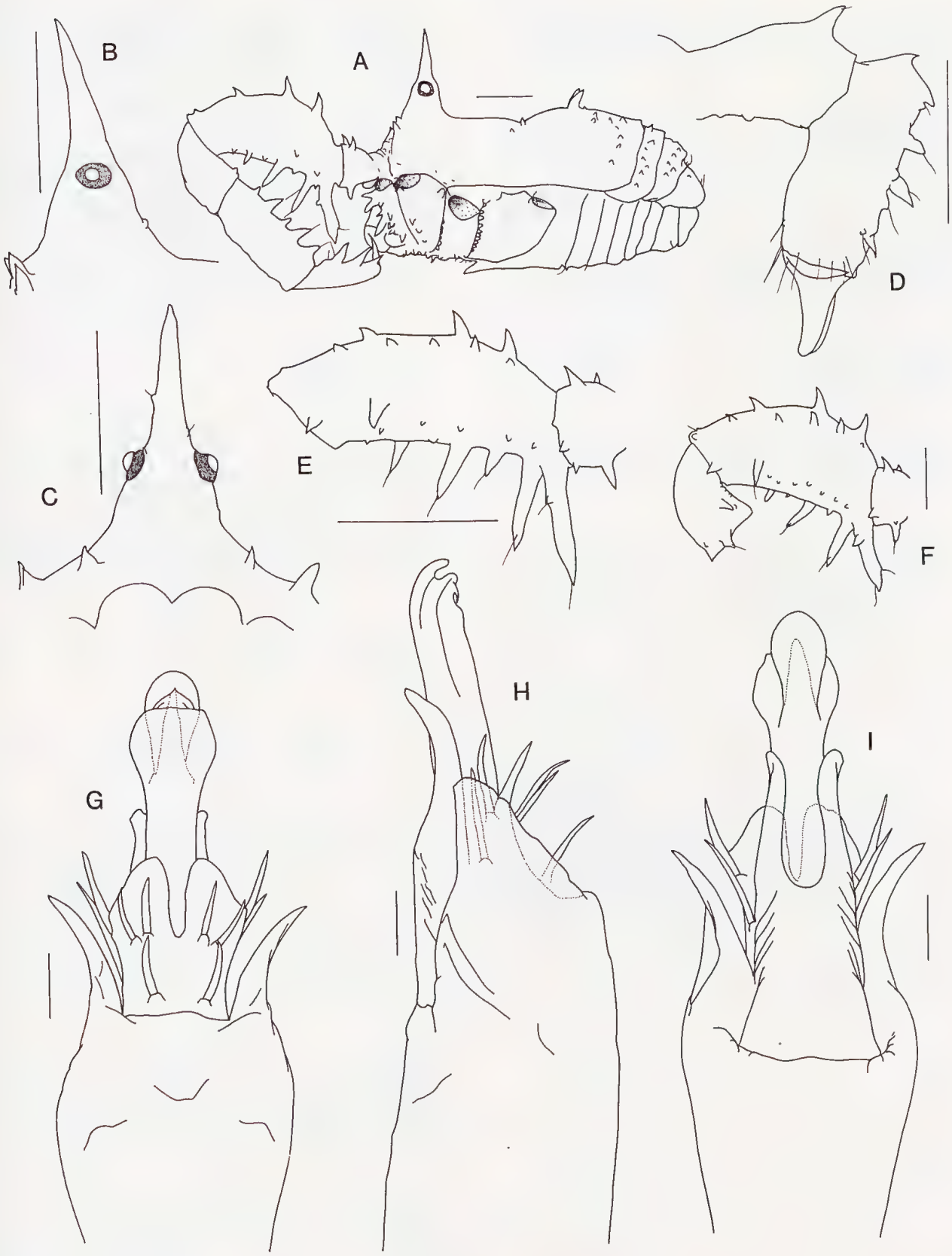


**Fig.6.** *Hickmanoxyomma goedei* n.sp. A = Holotype male; D, F–I = male KS19747 ; E = female KS19765. A = body and pedipalp, lateral; B, C = eyemound, lateral and frontal; D = chelicera, retrolateral, E–F = pedipalp femur, prolateral (male at reduced scale); G–I = distal part of penis, ventral, lateral & dorsal. Scale bars: A–F = 1.0 mm; G–I = 0.1 mm.

(size order 1,3,4,2,5); calcaneus I about 0.25 astragalus; ventral plate about as long as wide, middle inferior setae close to and lateral to distal pair, notch deep, about 0.5 plate length and reaching beyond distal pair of inferior setae.

**Description.** MALE. *Body.* Dorsal colour yellow-dark brown; pigmentation pattern as figured, well developed. Eyemound rising just behind anterior margin; spine quite erect, SA about 80°, SH about 1.5 IOD; lateral flanks sloping steeply immediately below eyes. Anterior margin with 2 tubercles on each side, the mesial pair closer to the eyemound and larger than in *H. cavaticum*. TA3 with pair of gracile suberect spines; TA1 with pair small tubercles; TA2 lacking granules, TA4 with more widely spaced pair of tubercles; distribution of other granules as figured. At least 4 lateral sclerites seen in partially distended female. Genital operculum longer than wide; spiracle slightly obscured by tubercles on coxa IV.

*Chelicerae.* Prodistal spine on first segment moderately large; second segment without strong upwardly directed mound on proximodorsal surface, dorsal surface with strong proximal spine, 1 at about 0.3 and another at about 0.5.

*Pedipalps.* Long and gracile; ratio PF:CW 0.86. Femur with row of 3 mediodorsal spines (size order 2,1,3), 3–4 smaller prodorsal spines, and 4–5 retroventral spines (size order 1,3,4,2,5). Accessory denticles on proximoventral trifid spine weakly developed. Trifid spine and proximal retroventral spine only weakly joined at base. Tibia with 5 retroventral spines.

*Legs.* Ratio FIV:CW 2.48; CI:AI 0.24. Lateral branches on claw of legs III & IV small; juveniles with 2 pairs of branches. Tarsal formula: 5–6(2),15–18(2–3),4,4.

*Genitalia.* Ventral plate with 2 superior setae on each side, about as long as wide, widest subdistally and narrowing towards base. Middle inferior setae placed more distally and laterally than in *H. cavaticum*. Notch deep, about 0.5 plate length and reaching beyond distal pair of inferior setae. Lateral plate broad basally, obscuring bases of superior and proximal inferior setae, but relatively shorter than in *H. cavaticum*, terminating well below tips of superior setae. Glans terminally bifurcate in lateral view.

FEMALE. Differs from male as in *H. cavaticum*. Tarsal formula: 4(2)15–16(3),4,4.

**Measurements** (Scotts Peak sample, n = 3 males, 1 female).

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | |
| 4.59-5.12 | 3.13-3.33 | 2.54-3.13 | 4.36-4.67 | 1.05-1.10 | 9.71-10.10 | 0.76-0.91 | 8.42-8.52 | 2.40-2.61 | M |
| Mean | | | | | | | | | |
| 4.91 | 3.25 | 2.81 | 4.56 | 1.08 | 9.90 | 0.85 | 8.47 | 2.52 | M |
| 4.54 | 3.02 | 2.69 | 4.35 | 1.06 | 9.69 | 0.87 | 8.07 | 2.40 | F |
| Standard Deviation | | | | | | | | | |
| 0.23 | 0.09 | 0.24 | 0.14 | 0.02 | 0.16 | 0.07 | 0.04 | 0.09 | M |

**Variation.** Nicholls Range KS 20023 penis with supernumerary inferior seta on left side, its eyemound SH 1.66 IOD, and the spine at about 0.3 on the cheliceral second segment is smaller than in the Scotts Peak population. PF:CW 0.88, FIV:CW 2.80, CI:AI 0.27. Tarsal formulae: males 5–6(2),16–20(3),4,4; females 4–5(2), 16–18(3),4,4. Measurements for a Nicholls Range male:

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| 4.43 | 3.13 | 2.74 | 4.59 | 1.22 | 10.13 | 1.11 | 8.75 | 2.33 | M |

**Comments.** *Hickmanoxyomma goedei* is most closely related to *H. cavaticum* and *H. clarkei*. Electrophoretic work is planned to assess differences between the Scotts Peak and Nicholls Range populations.

**Etymology.** The specific epithet acknowledges the extensive cave fauna collecting program of cave geomorphologist Dr Albert Goede, University of Tasmania, including the first specimens of this species taken at Scotts Peak.

**Natural history.** At Nicholls Range most specimens were found in small fissure caves in the twilight zone (S. Eberhard, personal communication) whereas *Hickmanoxyomma* in general is more common in the dark zone (A. Goede, personal communication). It may be more likely to find Nicholls Range specimens on the surface. *Hickmanoxyomma goedei* is more strongly pigmented than *H. cavaticum* and may be a troglophile.

**Distribution.** Southern Tasmania: Scotts Peak and Nicholls Range cave regions.

### *Hickmanoxyomma clarkei* n.sp.

Figs 7,8

**Type material.** Southern Tasmania, Cracroft area, South Picton Range, Judds Cavern (King Billy Cave)(C1): HOLOTYPE male, TMAG, J1559, R. Eberhard, 2 June 1980. PARATYPES: TMAG, J2857, same data, 1 female; KS20128, A. Goede, 30 Jan. 1975, 1 female; KS20129, same data, 1 immature; KS20130, on wall beside stream, S. Eberhard, 5 Apr. 1988. Matchlight Cavern (C2): KS20131, A. Goede, 17 Jan. 1978, 1 female. Cave C6: TMAG, J1560, R. Eberhard, 3 June 1980, 1 male, 1 female.

**Additional material examined.** Southern Tasmania, Precipitous Bluff, Bauhaus Cave (PB6): KS20058, A. Clarke, 24 Dec. 1988, 2 males, 1 female; KS20059, same data, 1 female; KS20148, same data, 1 male, 1 female, 1 immature; KS20149, same data, 1 male.

**Diagnosis.** Eyemound spine very long, SH about 1.8 IOD; lateral flanks sloping steeply immediately below eyes. TA2 with a larger pair of tubercles than TAI; genital operculum longer than wide; pedipalp femur with 4–5 retroventral spines (size order 1,3,4,2,5). Proximal accessory denticle on proximoventral trifid spine moderately developed; calcaneus about 0.3 astragalus; ventral plate much longer than wide; notch about 0.3 plate

length and reaching only to distal inferior setae. Lateral plate broad basally and long, obscuring all setal bases and obscuring all or virtually all of proximal superior seta.

**Description.** MALE. *Body*. Dorsal colour yellow-dark brown; pigmentation pattern as figured, well developed. Eyemound rising just behind anterior margin; spine very erect, SA about 80°, spine very long, SH about 1.8 IOD; lateral flanks sloping steeply immediately below eyes. Anterior margin with 4 tubercles on each side. TA3 with pair of strong spines; TA1 with pair small tubercles; TA2 with a larger pair of tubercles, TA4 with more widely spaced pair; distribution of other granules as figured. 5 lateral sclerites easily seen in distended specimen. Genital operculum longer than wide; spiracle barely obscured by tubercles on coxa IV.

*Chelicerae*. Prodistal spine on first segment moderately large; second segment without strong upwardly directed mound on proximodorsal surface, dorsal surface with strong proximal spine and another towards middle.

*Pedipalps*. Long and gracile; ratio PF:CW 0.86. Femur with row of 3 mediodorsal spines (size order 1=2,3), 3 smaller prodorsal spines, and 4–5 retroventral spines (size order 1,3,4,2,5). Proximal accessory denticle on proximoventral trifid spine moderately developed. Trifid spine and proximal retroventral spine only slightly joined at

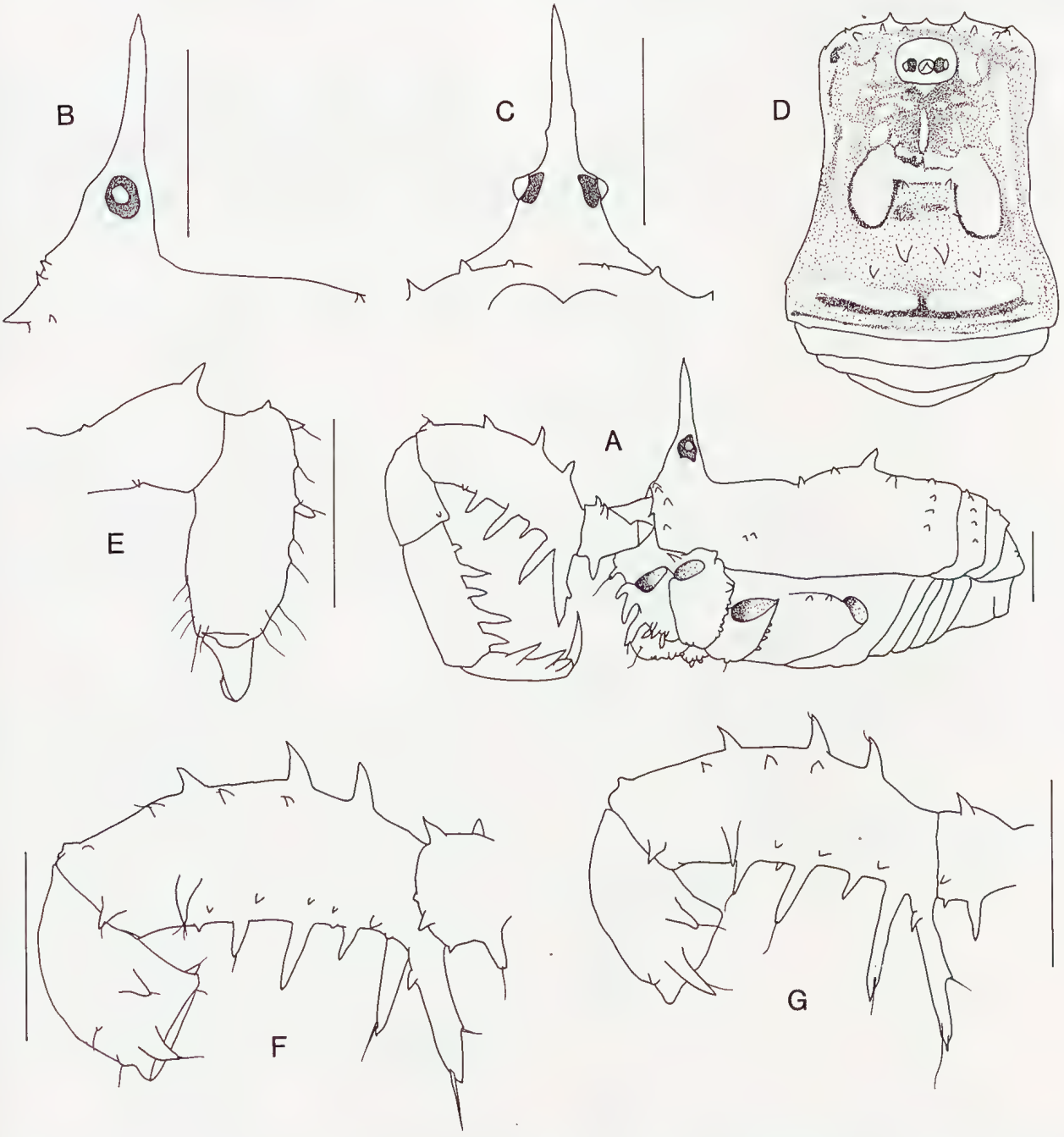


**Fig.7.** *Hickmanoxyomma clarkei* n.sp. A–F = Holotype male; G = female J2857. A = body and pedipalp, lateral; B, C = eyemound, lateral & frontal; D = body, dorsal; E = chelicera, retrolateral; F, G = pedipalp femur and patella, prolateral. Scale bars = 1.0 mm.

base. Tibia with 5 retroventral spines.

*Legs.* Ratio FIV:CW 2.82; ratio CI:AI 0.31. Lateral branches on claw of legs III & IV small; juveniles with 2 pairs of branches. Tarsal formula: 5–6(2),20–21(3),4,4.

*Genitalia.* Ventral plate with 2 superior setae on each side, much longer than wide, widest subdistally and narrowing towards base. Notch shallower than in *H. cavaticum*, about 0.3 plate length and reaching only to distal inferior setae. Lateral plate broad basally and long, when erect obscuring all setal bases and obscuring all or virtually all of proximal superior seta. Glans terminally cleft in lateral view.

FEMALE. Similar to male except: pedipalps more gracile, proximal accessory denticle on trifid spine weaker. Tarsal formula: 5(2),18–20(3),4,4.

**Measurements** (Cracroft sample, n = 2 males, 4 females).

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | |
| 4.56-4.60 | 3.16-3.19 | 2.63-2.83 | 4.53-4.66 | 1.40-1.42 | 10.34-10.74 | 1.21-1.30 | 8.83-9.11 | 2.26-2.28 | M |
| 3.96-5.56 | 2.97-3.47 | 2.46-2.94 | 4.40-4.74 | 1.31-1.46 | 9.75-10.76 | 1.24-1.32 | 8.47-9.28 | 2.28-2.40 | F |
| Mean | | | | | | | | | |
| 4.58 | 3.18 | 2.73 | 4.60 | 1.41 | 10.54 | 1.26 | 8.97 | 2.27 | M |
| 4.79 | 3.18 | 2.70 | 4.55 | 1.38 | 10.41 | 1.26 | 8.98 | 2.32 | F |
| Standard Deviation | | | | | | | | | |
| 0.53 | 0.18 | 0.17 | 0.12 | 0.06 | 0.35 | 0.04 | 0.28 | 0.05 | F |

**Variation.** Precipitous Bluff animals: bigger, PF:CW 1.03, FIV:CW 2.32, CI:AI 0.29, lack tubercle on TA2 though granule may be present, only 3 tubercles on anterior margin, retrolateral spine 4 on pedipalp femur poorly developed and pedipalp more granular. Tarsal formula: 6(2),16-17(3),4,4. Means for 2 males:

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| 5.77 | 3.82 | 3.93 | 4.78 | 1.38 | 10.39 | 1.29 | 8.85 | 3.01 | M |

**Comments.** *Hickmanoxymma clarkei* is similar to *H. eberhardi* in penis structure. The latter species, however, has apomorphic reductions in tergal spines and has lost the claw branches from legs III and IV. Electrophoresis will be used to assess differences in the

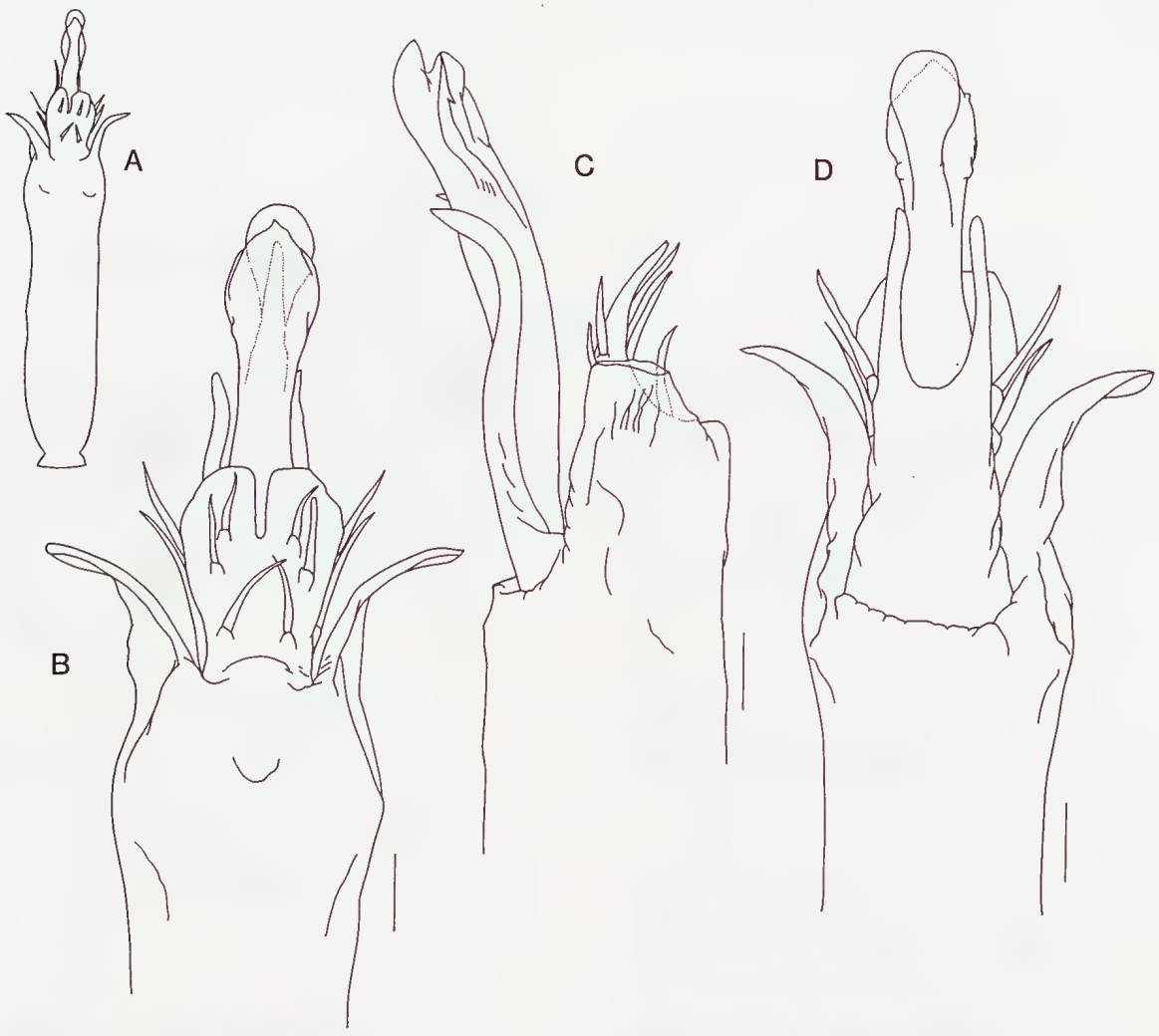


**Fig.8.** *Hickmanoxyomma clarkei* n.sp. Holotype penis: A = entire; B-D = distal part, ventral, lateral and dorsal. Scale bars: A = 1.0 mm; B-D = 0.1 mm.

Cracroft and Precipitous Bluff populations of *H. clarkei*.

**Etymology.** The specific epithet acknowledges the contribution made by Mr Arthur Clarke, Chairman of the Tasmanian Karst and Cave Research Group, to Tasmanian biospeleology, including collection of the first specimens of this species from Precipitous Bluff.

**Distribution.** Southern Tasmania, Cracroft and Precipitous Bluff karst areas.

### *Hickmanoxyomma eberhardi* n.sp.
Fig. 9

**Type material.** South-west Tasmania, Mount Anne, Col-In-Cavern Cave (MA1): HOLOTYPE male: KS19450, dark zone, S. Eberhard, 24 Jan. 1987. PARATYPES: KS20040, same data, 1 female; KS19449, S. Eberhard, 29 Jan. 1987, 1 male. MA14 Cave: KS20038, on walls below pitch 1, G. Smith, 20 Jan. 1987, 1 male; KS20039, same data, 1 female. Deep Thought Cave (MA10): KS20124, in crevice between pitches 1 & 2, G. Smith, 18 Jan. 1987, 1 male; KS20125, dark zone, 160 m depth, S. Eberhard, 13 Jan. 1987, 2 males, 1 female. Anne-A-Kananda Cave (MA9): KS20126, on walls below entrance chamber, L. Whaler and G. Smith, 19 Jan. 1987, 1 male, 1 female. Meltwater Pot Cave (MA20): KS20127, on wall, 60 m depth, S. Eberhard, 25 Jan. 1987, 2 females.

**Diagnosis.** Lateral flanks sloping gradually immediately below eyes; TA3 only with pair of very small mesial tubercles; genital operculum broader than long; 5 retroventral spines (size order 1,4,2,5,3); calcaneus I about 0.25 astragalus, claw on legs III & IV without lateral prongs; ventral plate about 1.25 as long as wide, notch about 0.4 plate length and not reaching most distal pair of inferior setae.

**Description.** MALE. *Body*. Dorsal colour straw yellow to very light brown; pigmentation pattern very faint. Eyes small, eye pigment reduced; eyemound rising just behind anterior margin; spine suberect, SA about 70°, SH about 1.45 IOD; lateral flanks sloping gradually immediately below eyes. Anterior margin with 2–3 tubercles on each side. TA3 and TA1 each with pair of very small tubercles; TA2 lacking even granules, TA4 with more widely spaced pair of tubercles; distribution of other granules as figured. 4–5 lateral sclerites easily seen in distended specimens. Genital operculum broader than long. Spiracle not obscured by brigding tubercles on coxa IV.

*Chelicerae*. Prodistal spine on first segment moderately large, smaller denticles more proximally; second segment without strong upwardly directed mound on proximodorsal surface, dorsal (anteriad)surface with strong proximal spine and another towards the middle.

*Pedipalps*. Long and gracile, more slender than in *H. cavaticum*; PF:CW 0.89. Femur with row of 3 mediodorsal spines (size order 2 = 3,1), 4–6 smaller prodorsal spines, and 5 retroventral spines (size order 1,4,2,5,3). Proximal accessory denticle on proximoventral trifid spine moderately developed. Trifid spine and proximal retroventral spine joined at base. Tibia with 5 retroventral spines.

*Legs*. Slender. Ratio FIV:CW 2.87; ratio CI:AI 0.25. Claw on legs III and IV without lateral branches in adult (juveniles not seen). First tarsal article long. Tarsal formula: 4–5(2),14–16(3),4,4.

*Genitalia*. Ventral plate with 2 superior setae on each side, about 1.25 as long as wide, widest subdistally and narrowing towards base, similar to that of *H. clarkei* in form but narrower. Notch relatively shallow, about 0.4 plate length and not reaching most distal pair of inferior setae. Lateral plate broad basally and obscuring setal bases on ventral plate; not obscuring tip of proximal superior seta. Glans terminally cleft in lateral view.

FEMALE. Differs from male as in *H. cavaticum*. Tarsal formula: 4(2),12–17(3),4,4.

**Measurements** (n = 5 males, 3 females).

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | |
| 3.39- | 2.36- | 2.01- | 3.75- | 1.17- | 8.05- | 1.00- | 7.22- | 1.69- | M |
| 4.13 | 2.86 | 2.55 | 4.32 | 1.40 | 8.89 | 1.24 | 8.02 | 2.17 | |
| 3.75- | 2.51- | 2.07- | 3.90- | 1.25- | 8.29- | 1.07- | 7.44- | 1.97- | F |
| 4.19 | 2.81 | 2.41 | 4.33 | 1.40 | 9.27 | 1.28 | 7.99 | 2.07 | |
| Mean | | | | | | | | | |
| 3.72 | 2.63 | 2.33 | 4.08 | 1.26 | 8.53 | 1.14 | 7.54 | 1.96 | M |
| 4.02 | 2.64 | 2.21 | 4.06 | 1.34 | 9.00 | 1.16 | 7.69 | 2.01 | F |
| Standard Deviation | | | | | | | | | |
| 0.27 | 0.20 | 0.20 | 0.19 | 0.09 | 0.30 | 0.08 | 0.28 | 0.18 | M |
| 0.19 | 0.13 | 0.15 | 0.19 | 0.07 | 0.20 | 0.09 | 0.23 | 0.04 | F |

**Comments.** This species seems to be most closely related to one or more undescribed species represented only by females from the Bubs Hill, Andrews River and Franklin River karst areas in south-west Tasmania. These show reduction in the spine on TA3 but retain lateral branches on leg claws. *Hickmanoxyomma eberhardi* is the second most cave adapted species after *H. cristatum*, although subdivision of leg tarsi is only moderate. Its similarity to *H. cristatum* in reduction of spines on TA3 and loss of lateral branches on tarsal claws is regarded as convergence.

**Etymology.** The specific epithet acknowledges the large numbers of harvestmen collected by biospeleologist Mr Stephan Eberhard in Tasmanian caves, including caves in Mount Anne.

**Distribution.** Caves in Mount Anne, south-west Tasmania.

### *tasmanicum* species group

Two species, northern Tasmania, surface and cave dwelling. Ventral plate widest basally, 1 superior seta; lateral plate narrow basally; end of glans may be slightly concave but not deeply cleft in lateral view; free lateral

**Fig.9.** *Hickmanoxyomma eberhardi* n.sp. A = Holotype male; B–C, F = male KS20038; G–I = male KS19449; D = female KS20039. A = body & pedipalp, lateral; B, C = eyemound, lateral and frontal; D, E = pedipalp femur and patella, prolateral, male with posterior enlargement of ventroproximal spines; F = chelicera, retrolateral; G–I = distal part of penis, ventral, lateral and dorsal. Scale bars: A–F = 1.0 mm; G–I = 0.1 mm.

sclerites apparently absent; chelicera second segment with strong upwardly directed proximal mound; SA usually less than 65°, CI:AI usually less than 0.24.

### *Hickmanoxyomma tasmanicum*

(Roewer, 1915) n.comb.

Figs 10,11

*Monacanthobunus tasmanicus* Roewer, 1915: 104–105; 1923: 604.
*Monoxyomma silvaticum* Hickman, 1958: 65–66. n.syn.

**Type material.** Tasmania: HOLOTYPE female: FIS, Roewer coll. no. 1034.

**Additional material examined.** North-east Tasmania: Holotype male and Allotype female (*M. silvaticum*) AM KS6925 & KS17635, Weldborough Pass, V.V. Hickman, 16 Apr. 1954. KS20135, Scottsdale, granite cave, A. Goede, 25 Oct. 1970, 1 immature male. KS20036, Lottah, mine adit on Anchor Lease, T. Goede, 24 Oct. 1970, 1 male, 1 female. KS20037, Flowery Gully Cave (FG201), Flowery Gully, 41°15'S, 146°50'E, R. Eberhard, 28 Feb. 1987, 1 male, 1 female.

**Diagnosis.** Lateral flanks of eyemound sloping gradually immediately below eyes, SA less than 50°; TA3 with pair of blunt spines with broad bases, mesial tubercles

**Fig.10.** *Hickmanoxyomma tasmanicum* (Roewer). A, E, G, I = holotype of *M. silvaticum*; B = holotype female, F, H = allotype female of *M. silvaticum*; C–D = Scottsdale male KS20036. A = body and pedipalp, lateral; B = lateral profile; C, E–F = eyemound, lateral; D = eyemound, frontal; G = chelicera, retrolateral; I–H = pedipalp (part), prolateral, male with posterior enlargement of ventroproximal spines. Scale bars = 1.0 mm.

on TA5 and free tergites large and rounded; dorsal surface of cheliceral second segment with proximal spine and a very strong spine towards the middle; pedipalp femur with 4 retroventral spines (size order 1,3,2,4), proximal accessory denticle on proximoventral trifid spine very strong; calcaneus I about 0.23 astragalus, distitarsus 2 with 4 articles; ventral plate about 0.85 as long as wide, notch about 0.5 plate length and reaching distal pair of inferior setae.

**Redescription.** MALE. *Body*. Dorsal colour reddish brown with dark brown reticulations. Eyemound rising just behind anterior margin; spine directed forwards, SA about 40°, spine relatively short, SH subequal to IOD; lateral flanks sloping gradually immediately below eyes. Anterior margin with 3 small tubercles on each side. TA3 with pair of blunt spines with broad bases, tubercle on TA2 larger than on TA1, TA4 with more widely spaced pair of tubercles, mesial tubercles on TA5 and free tergites large and rounded; distribution of other granules as figured. No lateral sclerites seen in distended specimens. Genital operculum circular. Spiracle not obscured by bridging tubercles but close to coxa IV.

*Chelicerae*. Prodistal spine on first segment very large; second segment with strong upwardly directed mound on proximodorsal surface, dorsal (anteriad) surface with proximal spine and a very strong spine towards the middle.

*Pedipalps*. Robust; ratio PF:CW 0.97. Femur with row of 4 mediodorsal spines (size order 1 = 2,3,4), 3 smaller prodorsal spines, and 4 retroventral spines (size order 1,3,2,4). Proximal accessory denticle on proximoventral trifid spine very strong. Trifid spine and proximal retroventral spine barely joined at base. Tibia with 5 retroventral spines (1, 3 and 5 shortest), granulate ventrally.

*Legs*. Relatively much shorter than in *H. cavaticum*, ratio FIV:CW 1.70; ratio CI:AI 0.23. Claw on legs III and IV with longer lateral branches than in *H. gibbergunyar* n.sp., juveniles with 3 pairs. Tarsal formula: 4–6(2),15–18(4),4,4.

*Genitalia*. Ventral plate with 1 superior seta on each side, about 0.85 as long as wide, widest basally. Notch moderately deep, about 0.5 plate length and reaching distal pair of inferior setae. Lateral plate very narrow basally, not obscuring bases of any setae. In lateral view, glans without terminal concavity and not cleft.

FEMALE. The holotype female closely resembles males in the specific characters including the characteristic spines on TA3. The eyemound spine is slightly more erect, SA about 50°. Otherwise females differ from males as in *H. cavaticum*. Tarsal formula: 4(2),13–16(3–4),4,4.

**Measurements** (north-east Tasmania excluding Flowery Gully, n = 2 males, 3 females).

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | |
| 4.41-4.59 | 2.84-3.01 | 2.81-2.86 | 2.63-2.68 | 0.59-0.62 | 5.56-5.65 | 0.54-0.70 | 4.93-5.02 | 2.39-2.42 | M |
| 3.71-4.27 | 2.44-2.76 | 1.91-2.11 | 2.13-2.73 | 0.56-0.63 | 4.55-5.84 | 0.45-0.55 | 3.93-5.23 | 1.79-2.10 | F |
| Mean | | | | | | | | | |
| 4.50 | 2.92 | 2.84 | 2.66 | 0.60 | 5.61 | 0.62 | 4.97 | 2.40 | M |
| 4.07 | 2.60 | 2.02 | 2.43 | 0.59 | 5.13 | 0.50 | 4.54 | 1.96 | F |
| Standard Deviation | | | | | | | | | |
| 0.25 | 0.13 | 0.09 | 0.25 | 0.03 | 0.54 | 0.04 | 0.53 | 0.13 | F |

**Variation.** The holotype has relatively shorter legs than other females. There is slight variation in the angle and length of the eyemound spine. The Lottah male KS20036 has a very robust spine.

The ventral plate of the Flowery Gully Cave specimen

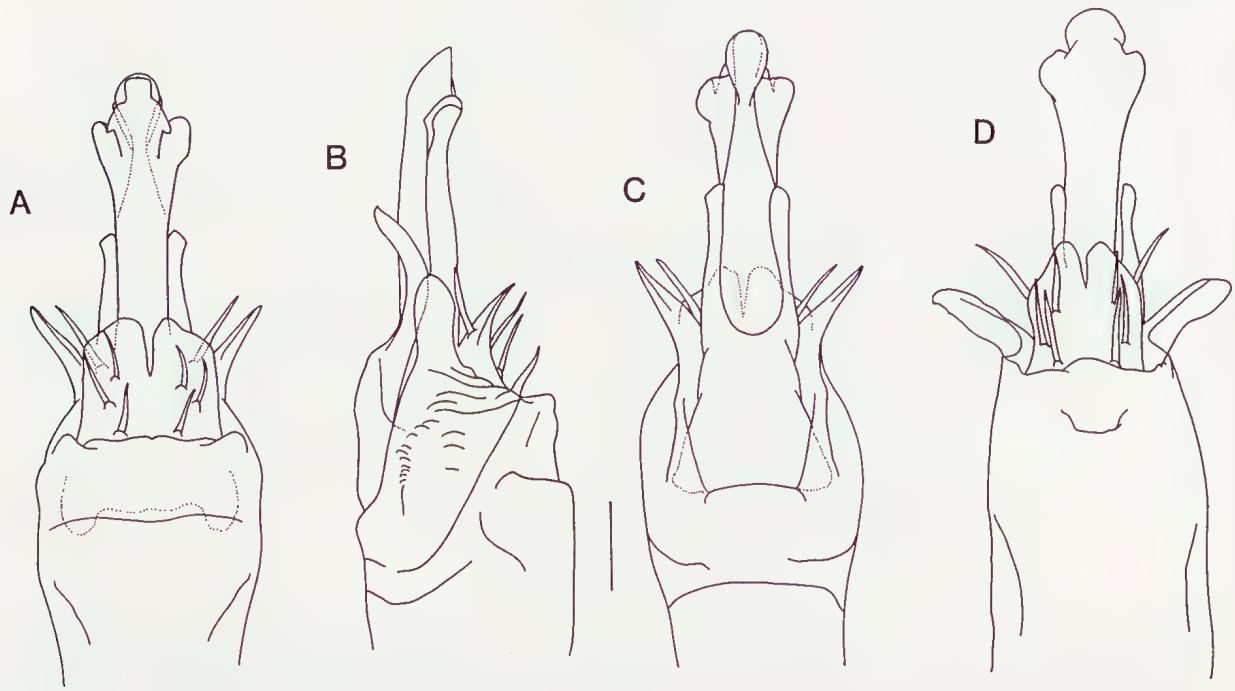


**Fig.11.** *Hickmanoxyomma tasmanicum* (Roewer). Distal part of penis: A-C, holotype of *M. silvaticum*, ventral, lateral, dorsal; D = Flowery Gully, ventral. Scale bar = 0.1 mm.

is relatively narrow. Measurements of the male and female from Flowery Gully Cave are:

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| 3.76 | 2.43 | 2.08 | 2.69 | 0.50 | 5.30 | 0.56 | 4.52 | 1.73 | M |
| 4.13 | 2.67 | 2.18 | 2.77 | 0.42 | 5.49 | 0.52 | 4.85 | 1.92 | F |

The legs are marginally longer than surface individuals from other populations. Tarsal formula: male 5(2), 15–16(4),4,4; female 4(2),15–16(5),4,4. The body is heavily pigmented; no troglomorphies are noted.

**Comments.** Hickman's types of *M. silvaticum* show close identity to Roewer's holotype female (precise locality not specified), particularly in possessing the distinctively shaped spines on TA3 and four articles in distitarsus II. Hence *M. silvaticum* is synonymised with *H. tasmanicum*. Electrophoretically, the Flowery Gully Cave sample (n = 1) differs from the Weldborough Pass sample (n = 1) in 6 out of 12 enzymes studied, GD = 0.672 (D. Coglan, personal communication). This is highly suggestive of a specific difference. Until larger samples are available, the Flowery Gully population is provisionally placed in *H. tasmanicum* because of morphological similarities.

*Hickmanoxyomma tasmanicum* is the only species in the genus which has retained the typical number of three lateral branches on hind claws, emphasising its epigean status.

**Natural history.** Though not primarily a cavernicole this species has been collected in a limestone cave, a small granite cave and a mine adit. The legs of surface specimens are relatively longer and have more tarsal articles than the closely related *O. saltuensis* suggesting some degree of "preadaptation" to cave life.

**Distribution.** North-east Tasmania, east of Tamar River in Scottsdale-Weldborough area, and Flowery Gully Caves immediately west of Tamar River.

### *Hickmanoxyomma gibbergunyar* n.sp.
Fig. 12

**Type material.** Northern Tasmania, Mole Creek, 41°32'S, 146°20'E: HOLOTYPE male: KS20031, Baldocks Cave (MC32), A. Goede, 20 Feb. 1972. PARATYPES: Baldocks Cave: KS20032, same data, 1 female; KS20132, same data, 2 males; KS20133, A. Goede, 15 Nov. 1969, 1 male. Honeycomb Cave (MC84): QVM, 1989/13/2, Type 442, T. Churchill, 17 Mar. 1988, 1 female. Wet Cave (MC144): QVM, 1989/13/3 Type 444, T. Churchill, 18 Oct. 1987, 1 immature. Herberts Pot cave (MC202): TMAG, J2861, R. J. Cockerill, 9 June 1968, 1 male; Cow Cave-Pyramid Cave link: TMAG, J2860, R.J. Cockerill, 12 Apr. 1968, 1 female. Westmoreland Cave (MC-X64): KS20134, R.J. Cockerill, 27 Jan. 1968, 1 male, 1 female. Caves (unspecified): QVM, 1989/13/3 Type 443, V.L. Fahey, 8 Jan. 1986, 1 male; QVM, 1989/13/1 Type 441, 2 km South Mole Creek, 30 m in cave, K. Crocker, Aug. 1981, 1 male.

**Diagnosis.** Lateral flanks of eyemound sloping steeply immediately below eyes, SA greater than 50°; TA3 with pair of large sharp spines; dorsal surface of cheliceral second segment with proximal spine and 2 others towards the middle; pedipalp femur with row of 4 mediodorsal spines, 5 retroventral spines (size order 1,5 = 3,4,2), tibia with 4 retroventral spines; calcaneus I about 0.15 astragalus; ventral plate about 1.2 as long as wide, notch not reaching most distal pair of inferior setae.

**Description.** MALE. *Body.* Dorsal colour light brown with darker brown patterning; pigmentation pattern faint but includes mesial saddle-shaped stripe. Eyemound rising just behind anterior margin; spine suberect, SA about 65°, spine relatively short, SH about 1.15 IOD; lateral flanks sloping steeply immediately below eyes. Anterior margin with 2-3 tubercles on each side. TA3 with pair of large sharp spines, tubercle on TA2 larger than granule on TA1, TA4 with more widely spaced pair of tubercles; distribution of other granules as figured. No lateral sclerites seen in distended specimens. Genital operculum circular. Spiracle not obscured by brigding tubercles but very close to coxa IV.

*Chelicerae.* Prodistal spine on first segment very large; second segment with strong upwardly directed mound on proximodorsal surface, dorsal (anteriad) surface with proximal spine and 2 others towards the middle.

*Pedipalps.* Long, ratio PF:CW 0.99. Femur with row of 4 mediodorsal spines (size order 2,1 = 3,4), 5 smaller prodorsal spines, and 5 retroventral spines (size order 1,5 = 3,4,2). Both accessory denticles on proximoventral trifid spine moderately developed. Trifid spine and proximal retroventral spine barely joined at base. Tibia with 5 retroventral spines (3 shortest, 1 and 5 less so).

*Legs.* Ratio FIV:CW 2.15; calcaneus short, ratio CI:AI 0.15. Femur I very tuberculate, particularly dorsally. Claw on legs III and IV with 1 pair of small lateral branches, juveniles with 2 pairs. Tarsal formula: 4(2),14–16(3–4),4,4.

*Genitalia.* Ventral plate with 1 superior seta on each side, about 1.20 as long as wide, widest basally. Notch relatively shallow, about 0.3 plate length and not reaching most distal pair of inferior setae. Lateral plate narrow basally, not obscuring bases of inferior setae. In lateral view glans with terminal concavity but not cleft.

FEMALE. Differs from male as in *H. cavaticum*. Tarsal formula: 3(2),12–14(3),4,4.

**Measurements** (Baldocks Cave sample, n = 4 males, 1 female).

| | SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | | |
| | 5.16-6.43 | 3.39-3.73 | 3.33-3.91 | 4.80-5.08 | 0.73-0.77 | 9.44-9.96 | 0.76-0.84 | 7.47-8.21 | 2.90-3.38 | M |
| Mean | | | | | | | | | | |
| | 5.86 | 3.62 | 3.60 | 5.00 | 0.75 | 9.70 | 0.79 | 7.77 | 3.14 | M |
| | 5.18 | 3.30 | 2.80 | 4.49 | 0.70 | 9.00 | 0.67 | 7.35 | 2.60 | F |
| Standard Deviation | | | | | | | | | | |
| | 0.46 | 0.14 | 0.21 | 0.12 | 0.02 | 0.23 | 0.03 | 0.27 | 0.17 | M |

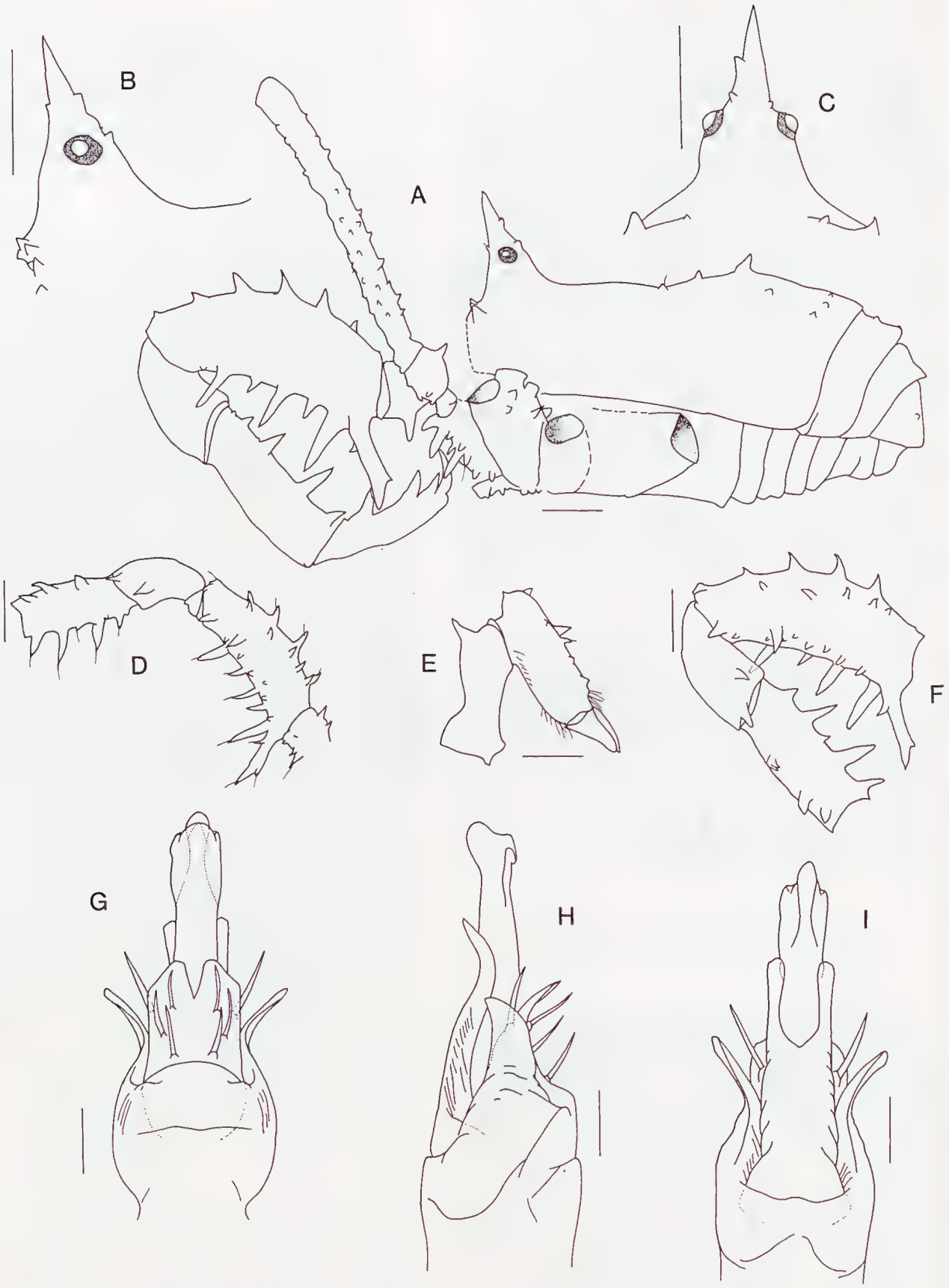


**Fig.12.** *Hickmanoxyomma gibbergunyar* n.sp. A = Holotype male; C, F–I = male KS20023; D = female KS20032. A = body, pedipalp and femur I, lateral; B, C = eyemound, lateral and frontal; D, F = pedipalp femur and patella, prolateral; E = chelicera, retrolateral; G–H = distal view of penis, ventral, lateral and dorsal. Scale bars: A–F = 1.0 mm; G–I = 0.15 mm.

**Variation.** A male and female from Westmoreland Cave had the following measurements:

| SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|
| 6.86 | 4.30 | 4.28 | 5.35 | 0.74 | 10.08 | 0.67 | 7.85 | 3.68 | M |
| 6.24 | 3.84 | 3.47 | 4.64 | 0.67 | 8.93 | 0.65 | 7.15 | 3.10 | F |

**Comments.** *Hickmanoxyomma gibbergunyar* is most closely related to *H. tasmanicum*. The terminal part of the glans resembles that in *O. saltuensis*.

**Etymology.** The specific epithet is a noun in apposition from the Australian Aboriginal word "gibber-gunyar" which means "a cave dwelling".

**Distribution.** Central north Tasmania: Mole Creek Caves.

### *cristatum* species group

One species, southern Tasmania, cavernicolous. Ventral plate widest basally, 1 superior seta; lateral plate narrow basally; glans with broad crestlike termination in lateral view; lateral sclerites apparently lacking; chelicera second segment without upwardly directed proximodorsal swelling; pedipalp tibia with 5 retroventral spines; SA greater than 80°, CI:AI greater than 0.4 less than 0.7.

### *Hickmanoxyomma cristatum* n.sp.
Fig. 13

**Type material.** Southern Tasmania, Precipitous Bluff, 43°30'S, 146°35'E: HOLOTYPE male: KS19766, Quetzacoatl Conduit Cave (PB3), S. Eberhard, 29 Mar. 1986. PARATYPES: Quetzacoatl Conduit: KS19767, same data, 1 female; KS20022, K. Kiernan, 20 Jan. 1973, 2 immature; KS20057, A. Clarke, Dec. 1988, 1 female. Damper Cave (PB1): KS19769, A. Goede, 24-25 Jan. 1978, 4 females. Cueva del Blance cave: KS19768, S. Eberhard, 31 Mar. 1986, 1 male, 1 immature.

**Diagnosis.** Lateral flanks of eyemound sloping steeply immediately below eyes; anterior margin with 1 large tubercle on each side; TA1,2,3 each with pair of small granules; lateral sclerites apparently lacking; pedipalp femur with 4 retroventral spines (size order 1,4,2,3); calcaneus I about 0.5–0.6 astragalus, tarsal claw on legs III & IV without lateral prongs in adults and juveniles; ventral plate about 0.7 as long as wide, widest basally, notch not reaching most distal pair of inferior setae; lateral plate narrow basally, not obscuring inferior setal bases; in lateral view glans terminating in complex crestlike structure.

**Description.** MALE. *Body*. Dorsal colour yellow; pigmentation pattern very faint. Eyes small, eye pigment reduced; eyemound rising just behind anterior margin; spine very long and almost erect, SA about 85°, SH about 1.75 IOD; lateral flanks sloping steeply immediately below eyes. Anterior margin with 1 large tubercle on each side. TA1,2,3 each with pair of small granules, TA4 with more widely spaced pair; no lateral sclerites seen in 2 semidistended specimens. Genital operculum and base of sternum broader than in *H. cavaticum*, not obscured by the single retrolateral tubercle on coxa IV.

*Chelicerae*. Prodistal spine on first segment relatively small; second segment without strong upwardly directed mound on proximodorsal surface, dorsal (anteriad) surface with proximal spine and a stronger spine towards the middle.

*Pedipalps*. Long and gracile, similar to *H. eberhardi*, ratio PF:CW 1.25. Femur with row of 3 mediodorsal spines (size order 2,1 = 3), 3 smaller prodorsal spines, and 4 retroventral spines (size order 1,4,2,3). Proximal accessory denticle on proximoventral trifid spine weakly developed. Trifid spine and proximal retroventral spine joined at base though not as strongly as in *Odontonuncia*. Tibia with 5 retroventral spines (1 and 3 very short).

*Legs*. Very long, ratio FIV:CW 3.24; calcaneus very long, ratio CI:AI 0.58. Tarsal claw on legs III & IV without lateral branches in both adults and juveniles. Tarsal formula: 6(2),18–19(3),4,4.

*Genitalia*. Ventral plate with 1 superior seta on each side, about 0.7 as long as wide, widest basally. Notch prominent but relatively shallow, about 0.4 plate length and not reaching most distal pair of inferior setae. Lateral plate relatively narrow basally, not obscuring inferior setal bases on ventral plate. In lateral view glans strongly bent and expands terminally into complex crest-like structure.

FEMALE. Larger than male; otherwise differs as in *H. cavaticum*. Tarsal formula: 4–6(2),17–20(3),4,4.

**Measurements** (n = 2 males, 3 females).

| | SL | CW | PF | AI | CI | AIV | CIV | FIV | CSL | |
|---|---|---|---|---|---|---|---|---|---|---|
| Range | | | | | | | | | | |
| | 3.63-3.75 | 2.59-2.77 | 2.46-4.23 | 3.70-3.76 | 2.14-2.23 | 8.29-8.83 | 2.14-2.17 | 8.39-9.00 | 1.92-2.03 | M |
| | 4.00-4.78 | 2.71-3.29 | 2.23-2.69 | 3.81-4.39 | 2.14-2.19 | 8.81-10.16 | 2.14-2.22 | 8.59-9.54 | 2.16-2.46 | F |
| Mean | | | | | | | | | | |
| | 3.69 | 2.68 | 3.34 | 3.73 | 2.18 | 8.56 | 2.16 | 8.70 | 1.97 | M |
| | 4.38 | 2.95 | 2.45 | 4.00 | 2.16 | 9.14 | 2.13 | 8.82 | 2.27 | F |
| Standard Deviation | | | | | | | | | | |
| | 0.32 | 0.25 | 0.19 | 0.28 | 0.03 | 0.74 | 0.08 | 0.52 | 0.14 | F |

**Comments.** The species appears to be closely related to the *tasmanicum* species group of northern Tasmania. Its similarity with *H. eberhardi* in reduction of spine on TA3 and loss of lateral prongs on tarsal claws is regarded as convergence. The distinctive structure of the glans separates it from its congeners.

**Natural history.** This is the most troglomorphic species in *Hickmanoxyomma* and is almost certainly a troglobite.

**Etymology.** The specific epithet refers to the crest-like termination to the penis.

**Distribution.** Southern Tasmania, known from three

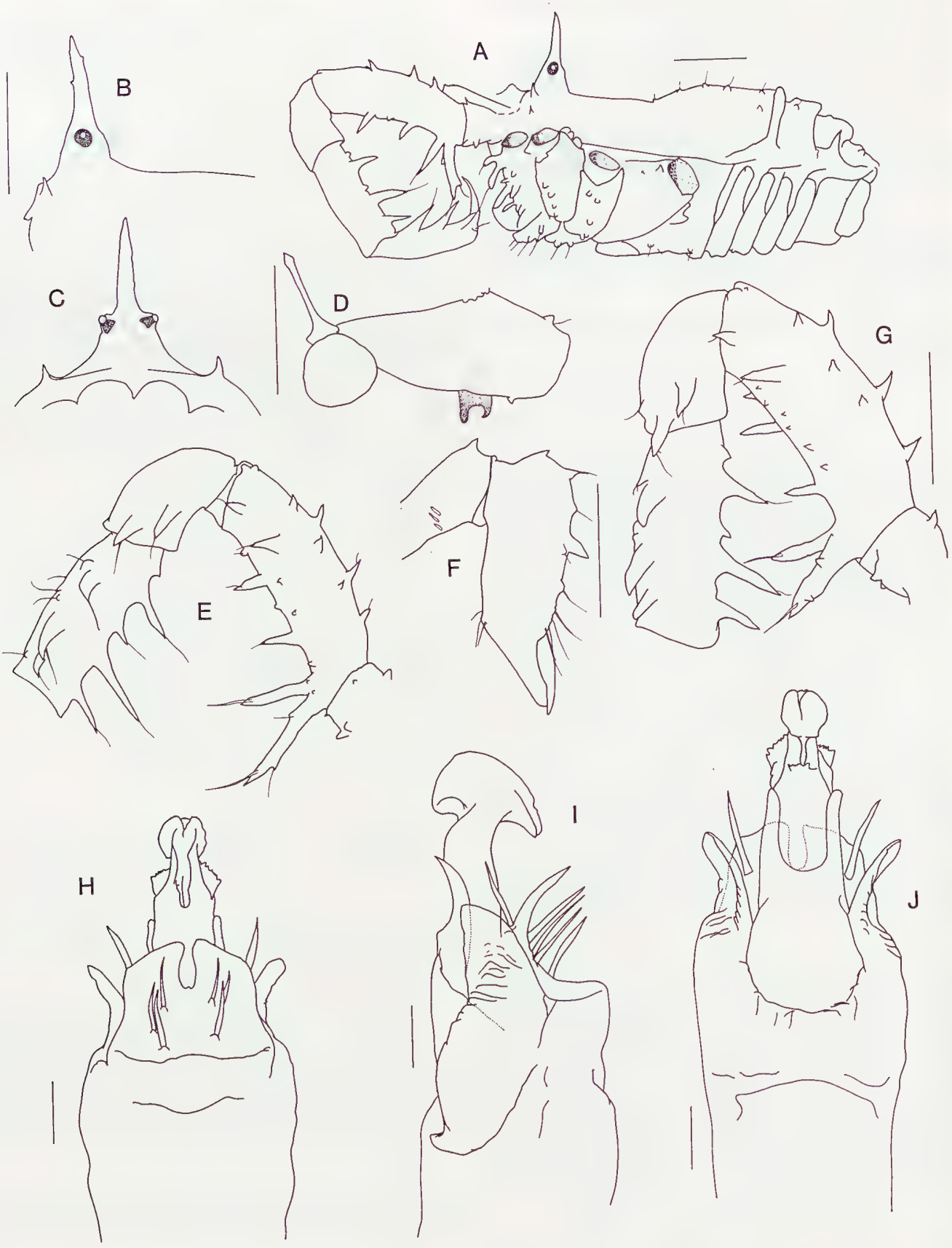


**Fig.13.** *Hickmanoxyomma cristatum* n.sp. A, D = Holotype male; B–C, F–J = male KS19768; E = female KS19767. A = body and pedipalp, lateral; B, C = eyemound, lateral and frontal; D = sternogenital region with coxa IV, E, G = pedipalp femur and patella, prolateral; F = chelicera, retrolateral; H–J = distal view of penis, ventral, lateral and dorsal. Scale bars: A–G = 1.0 mm; H–J = 0.1 mm.

caves at Precipitous Bluff. Apparently absent from Bauhaus Cave where it is replaced by a population of *H. clarkei*.

## Discussion

Cavernicolous species in *Hickmanoxyomma* have been reported from virtually all karst areas in Tasmania subjected to biospeleological examination (Eberhard, 1988; Clarke, 1988). A notable exception is the Junee-Florentine karst in central southern Tasmania where a troglomorphic *Nuncioides* sp. is established (J.L. Hickman, personal communication).

Cavernicolous *Hickmanoxyomma* spp. exhibit, in varying extent, adaptations to the cave environment: depigmentation, attenuation of pedipalps and legs, reduction in eye size (but not loss), reduced sclerotisation, reduction in size of tergal spines, reduction in size or loss of lateral prongs on claws of legs III and IV in adults, reduction in number or loss of lateral prongs in juveniles, an increase of articles in leg tarsi, and elongation of leg tarsal setae and claws.

The most troglomorphic species are *H. eberhardi* and *H. cristatum* which can probably be regarded as obligate cavernicoles, or troglobites. The most notable troglomorphy is the loss of lateral claw prongs from the hind legs of both adults and juveniles.

The balance of evidence suggests other troglomorphic species are also troglobites, though two circumstances leave room for doubt: 1. The Nicholls range population of *H. goedei* is relatively strongly pigmented and individuals frequent the entrance and twilight zones of small fissure caves. A population may live on the surface, e.g. in large logs. 2. Two individuals from the Hastings population of *H. cavaticum* have been collected under logs over 100 m from the nearest known cave entrance. Mesocavities in or under logs of the southern Tasmanian forests virtually reproduce the cave environment on the surface.

Evidence pointing to troglobitic status includes:

1. Gene flow across the surface at Hastings appears limited: preliminary allozyme studies suggest that the Hastings and North Lune populations might well be genetically isolated despite being only 3 km apart, with no major intervening barrier except lack of caves.

2. Within the Precipitous Bluff karst, *H. cristatum* has been recorded from three caves, but not from Bauhaus Cave where a population of *H. clarkei* is established. This suggests at least two separate invasions of the cave environment and little migration between caves. Further work is required to substantiate the allopatry of these species.

3. Despite considerable collecting for harvestmen across southern Tasmania, the *cavaticum* and *cristatum* species groups have not been recorded on the surface outside karst areas, nor from the mine adits where Dr A. Goede has searched.

In northern Tasmania, the *tasmanicum* species group has been recorded on the surface and in caves. *Hickmanoxyomma tasmanicum* occurs in essentially karst free north-eastern Tasmania where it is typically found under logs. It has also been taken from a small granite cave and a mine adit. To the west of the Tamar River, *H. tasmanicum* has given rise to a population in a limestone cave at Flowery Gully. This population appears to be genetically distinct from surface populations to the east of the river and may well prove to be a separate species. *Hickmanoxyomma gibbergunyar* appears confined to caves at Mole Creek.

Apart from the situation noted in *H. tasmanicum*, the surface progenitors of the cave species are likely to be extinct, or perhaps survive as relicts in a few favourable localities.

Extinction of the surface fauna may have facilitated speciation in cavernicolous *Hickmanoxyomma*. Such a model is favoured by Barr & Holsinger (1985) to explain speciation in many relictual temperate cavernicoles including spiders and predatory beetles, though these authors postulate interglacial warming and drying as the cause of surface extinctions.

In Tasmania, glacial climates of the Pleistocene which were cold, windy and dry may have been more important in causing epigean extinctions. Over ten areas of high altitude karst, for example Mount Anne where the highly troglomorphic *H. eberhardi* occurs, were at least partly over-ridden by glaciers, while several others including Mole Creek and Cracroft lay marginal to ice (Kiernan, 1982). North-eastern Tasmania had more equable climates and surface populations of *H. tasmanicum* and the closely related *O. saltuensis* survive only there.

The possible role of surface extinctions is less demonstrable for cavernicoles in the related genus *Holonuncia* which inhabits warmer latitudes on the mainland. Epigean relatives frequently occur in parapatry, or perhaps even sympatry.

It is possible that glaciation and periglacial conditions of central Tasmania facilitated isolation of the *tasmanicum* and *cavaticum* species groups respectively to the north and south. The two groups differ in many features and have been evolving separately for a considerable period, a conclusion supported by multiple fixed allozymic differences between *H. tasmanicum* and *H. cavaticum* (GD range 0.779–1.407, D. Coglan, personal communication). The aberrant *H. cristatum* in the extreme south of Tasmania, however, appears to be more closely related to the *tasmanicum* species group suggesting that the latter was once more widespread. It may have given rise to the *cavaticum* group through evolution of presumed apomorphies including a more elevated eyemound and two superior setae and an invaginated glans on the penis. Continued molecular systematic work will hopefully clarify these relationships.

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Hickman who permitted me to study his collection and extended great hospitality to me. Dr Albert Goede and Mr Stephan Eberhard, University of Tasmania, and Mr Arthur Clarke, Tasmanian Karst and Cave Research Group, have made extensive collections of Tasmanian cave Opiliones and accompanied me on fieldwork in Tasmania. Dr Mike Gray, Australian Museum, has given much encouragement, and advice on the manuscript, while Mr Roger Springthorpe assisted with illustrations and Mr Gerard Clark helped with a computer program which assisted measurements. The anonymous referees provided many constructive suggestions.

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# The Nereididae (Polychaeta) from Australia — Gymnonereidinae sensu Fitzhugh, 1987: *Australonereis, Ceratocephale, Dendronereides, Gymnonereis, Nicon, Olganereis* and *Websterinereis*

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ABSTRACT. The subfamily Gymnonereidinae (*sensu* Fitzhugh, 1987) is represented in Australian waters by 14 species in seven genera, of which five are new species and these are described: *Ceratocephale aureola* n.sp., *C. setosa* n.sp., *Gymnonereis minyami* n.sp., *G. yurieli* n.sp. and *Nicon rotunda* n.sp. Six species are new records for Australian waters. This subfamily of nereidids is characterised by the lack of chitinous pharyngeal papillae, although soft papillae may be present. A key to the subfamilies of the family Nereididae is given together with a key to the genera and Australian species of the subfamily Gymnonereidinae. This paper represents the first of a series which will describe the Australian nereidid fauna.

HUTCHINGS, P.A. & A. REID, 1988. The Nereididae (Polychaeta) from Australia. Records of the Australian Museum 42(1): 69–100.

The family Nereididae is well represented in Australian waters (Day & Hutchings, 1979) by 17 genera and approximately 67 species. During a study of nereidids from southern Australian waters (Hutchings & Turvey, 1982) it became apparent that many undescribed species existed in more tropical regions of Australia.

We have therefore undertaken a comprehensive study of Australian nereidids and this first paper considers the subfamily Gymnonereidinae *sensu* Fitzhugh (1987). Seven genera are represented: *Australonereis, Ceratocephale, Dendronereides, Gymnonereis, Nicon, Olganereis* and *Websterinereis*. We have followed the order of genera indicated in Fitzhugh's (1987, fig. 1) representation of phylogenetic relationships. We have examined all the nereidid material available in Australian State Museums and some material from ecological surveys lodged with various fisheries organisations. In this paper we describe 14 species of which five are new species and six new records for Australian waters. Fitzhugh (1987) has recently suggested that the subfamily Gymnonereidinae is a natural (=monophyletic) group which can be distinguished from the other two subfamilies, the Namanereidinae and the

Nereidinae due to the presence of biramous parapodia (distinguishing the group from the Namanereidinae) and the absence of paragnaths on the pharynx (unlike the Nereidinae). Soft papillae may be present on both or one of the pharangeal rings. The relationship between papillae and chitinous paragnaths is unclear, although the papillae often occur in a similar location and arrangement to paragnaths. Fitzhugh (1987) considers the absence of both papillae and paragnaths to be the plesiomorphic condition. Whilst the Gymnonereidinae always lack paragnaths, some members of the Nereidinae possess papillae in addition to paragnaths (for example *Leonnates*).

A recent study of the Namanereidinae indicates that papillae and sometimes paragnaths are indeed present in some species, thus confounding the current subfamily distinctions (Glasby, in preparation). In addition, whilst Fitzhugh (1987) suggests that both Gymnonereidinae and Namanereidinae are monophyletic, the other subfamily, the largest by far, the Nereidinae is a paraphyletic group. Thus the relationships of the three subfamilies to each other is unclear, and will require a far more detailed analysis of the Nereididae. Fitzhugh's (1987) analysis was based purely on the literature and a re-examination of the type species and revision of several problem genera is urgently needed before the relationship of these subfamilies may be further elicidated.

Within the Gymnonereidinae, as in the other subfamilies, the most important characters used to delineate genera include: presence or absence of branchiae; number of pairs of tentacular cirri; presence or absence of accessory dorsal and ventral cirri; ornamentation of the pharynx; number,shape and arrangement of the parapodial lobes and presence or absence of particular types of setae. Species within the genera are additionally distinguished by the arrangement and type of papillae within a particular area of the pharynx, and distribution and ornamentation of the setae as they occur along the body.

Within the nereidid literature a considerable number of terms have been used to describe the various component parts of the parapodia and setae. We have adopted the terminology proposed by Hylleberg *et al.* (1986) and Hylleberg & Nateewathana (1988), with minor changes (Fig. 1). We have two additional setal types, sesquigomph spinigers and falcigers (Fig. 1c,d). These are referred to as hemigomph by Fauchald (1977), who defined hemigomph as 'with asymmetrical articulation nearly at right angles to the long axis of the shaft'. We prefer to use the term sesquigomph to describe this type of seta, a term previously used by Perkins (1980). 'Sesqui' the Latin prefix for the ratio 3:2, refers to the approximate relationship between the boss and opposing prong of the shaft (as observed using the light microscope) rather than one half, implied by the term hemigomph.

Slight modifications to these terms are required for *Ceratocephale, Gymnonereis* and *Nicon*, and these are discussed in the Remarks Section after the relevant generic diagnoses.

The following measurements were recorded for animals examined, total body length, maximum body width excluding setae and parapodia, and the number of body segments. The Australian distribution of each species is indicated at the end of each species account. All existing records are indicated for species recorded from outside Australia.

The following abbreviations have been used in the text: AHF – Allan Hancock Foundation, Los Angeles, California (Polychaete collections now located at the Los Angeles County Museum); AM – Australian Museum, Sydney;

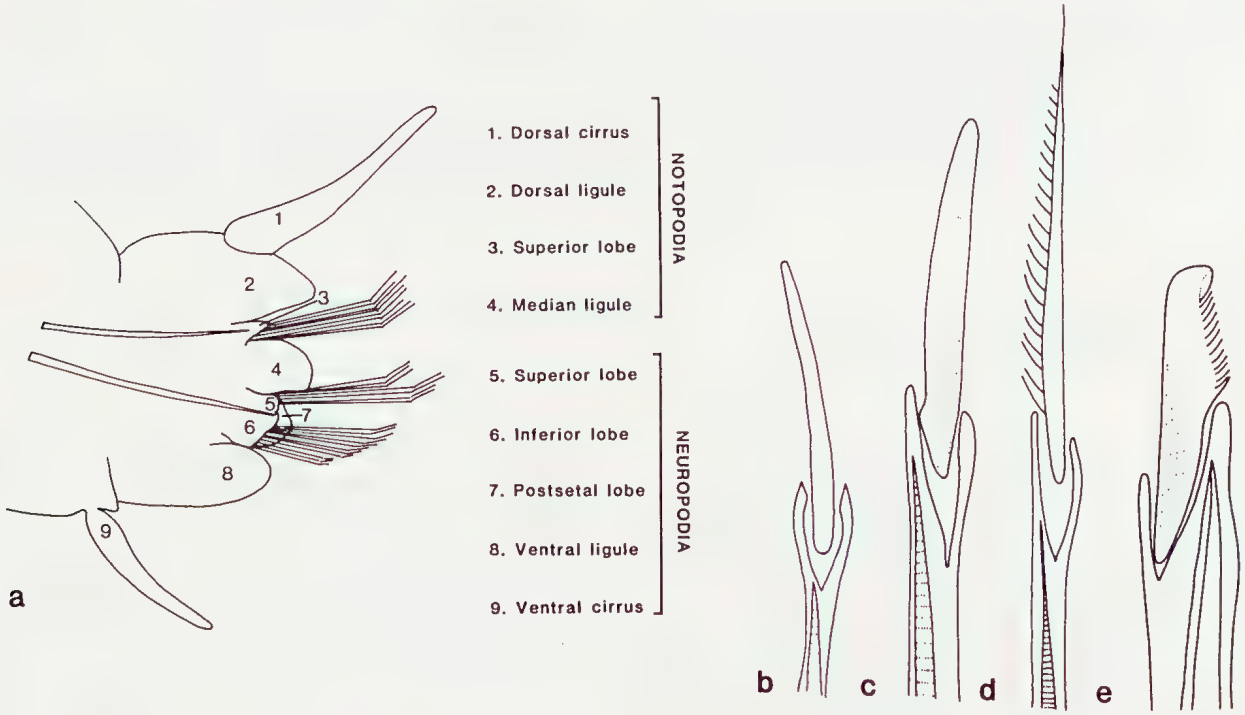


**Fig.1.** Terminology and diagram of a nereid parapodium; a, left parapodium, anterior view; b, homogomph falciger; c, sesquigomph falciger; d, sesquigomph spiniger; e, heterogomph falciger.

BMNH – British Museum (Natural History), London; NMV – National Museum of Victoria, now Museum of Victoria, Melbourne; NTM – Northern Territory Museum, Darwin; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide; TASM – Tasmanian Museum, Hobart; USNM – National Museum of Natural History, Smithsonian Institution, Washington, D.C.; WAM – Western Australian Museum, Perth.

The following abbreviations have been used in the tables: noto – notopodia; neuro – neuropodia; supra – supra-acicular fascicle; sub – subacicular fascicle; ho – homogomph; he – heterogomph; ses – sesquigomph; sp – spinigers; f – falcigers.

The specific names based on Aboriginal words were found by consulting 'Australian Aboriginal Words and Place Names and their Meanings' by Sydney E. Endacott (1984).

Tables referred to in the text are included in the Appendix.

## Taxonomy

After undertaking a phylogenetic study of the family, Fitzhugh (1987) has proposed three subfamilies within the family Nereididae: Nereidinae, Namanereidinae and the Gymnonereidinae. This classification has been adopted in this study.

### Key to the Subfamilies of Family Nereididae
(after Fitzhugh, 1987)

1. Paired antennae; 3–4 pairs tentacular cirri; pharynx lacking paragnaths and papillae; parapodia with reduced notopodia or without ligules ..... Namanereidinae

—— Paired antennae; 4 pairs tentacular cirri; pharynx with or without paragnaths or papillae; parapodia fully biramous ..... 2

2. Pharynx without chitinous paragnaths, papillae present or absent ..... Gymnonereidinae

—— Pharynx with chitinous paragnaths, papillae sometimes present in addition ..... Nereidinae

## Gymnonereidinae

Gymnonereidinae Banse, 1977: 611-613.—Fitzhugh, 1987: 174–183.

**Diagnosis.** Prostomium with paired antennae. Peristomium with 4 pairs of tentacular cirri. Papillae present or absent on proboscis; on oral and/or maxillary rings. Parapodia fully biramous, with ligules present in various combinations. Setae compound; noto- and neuropodial homogomph spinigers being most common, followed by neuropodial heterogomph falcigers.

### Key to Australian Gymnonereidinae*

1. Anterior ventrum with fleshy transverse ridges, maxillary ring with papillae, sometimes with horny tips ..... *Australonereis ehlersi*

—— Anterior ventrum without fleshy transverse ridges, pharynx with or without papillae ..... 2

2. Pharyngeal papillae present ..... 3

—— Pharyngeal papillae absent ..... *Nicon*, 12

3. Ventral cirri bifid ..... 4

—— Ventral cirri not bifid ..... 5

4. Dorsal cirri bifid in anterior parapodia ..... *Gymnonereis*, 6

—— Dorsal cirri not bifid ..... *Ceratocephale*, 7

5. Branchiae present ..... *Dendronereides*, 9

—— Branchiae absent ..... 10

6. Anterior parapodia with sesquigomph falcigers ..... *Gymnonereis minyami* n.sp.

—— Parapodia throughout with spinigers only ..... *Gymnonereis yurieli* n.sp.

7. Ventral cirri bifid from setiger 3 ..... *Ceratocephale setosa* n.sp.

—— Ventral cirri bifid from setiger 1 ..... 8

8. Eyes absent, all setae spinigers ..... *Ceratocephale ?pacifica*

—— Eyes present, sesquigomph falcigers in anterior setigers ..... *Ceratocephale aureola* n.sp.

9. Branchiae fine, tufted; pharynx Area V with 3–4 papillae, VI with 3–4 papillae ..... *Dendronereides heteropoda*

—— Branchiae fingerlike; pharynx Area V with 1 papilla, VI with 1–2 papillae ..... *Dendronereides zululandica*

10. Papillae on maxillary and oral rings ..... *Olganereis edmondsi*

—— Papillae on oral ring only ..... *Websterinereis*, 11

11. Neurosetae with few heterogomph spinigers posteriorly. Simple setae absent; notopodia and neuropodia not widely spaced ..... *Websterinereis foli*

—— Neurosetae with heterogomph spinigers throughout. Posterior parapodia with bifid simple setae in supra-acicular neuropodial fascicle; notopodia and neuropodia widely spaced in posterior setigers ..... *Websterinereis punctata*

12. Homogomph falcigers in supra-acicular neuropodial fascicle of anterior setigers ..... *Nicon rotunda* n.sp.

—— Homogomph falcigers absent ..... 13

13. Neurosetae homogomph spinigers and heterogomph falcigers; falcigers with long blades; neuropodial ligule anteriorly thick and rounded ..... *Nicon maculata*

—— Neurosetae with homogomph spinigers and heterogomph spinigers and falcigers; median neuropodial falciger blades with recurved distal tooth with distinct tendon; neuropodial ligule triangular ..... *Nicon moniloceras*

* This key is an artificial one and does not imply any phylogenetic relationships.

### *Nicon* Kinberg, emended

*Nicon* Kinberg, 1866: 178–179.—Pettibone, 1971: 7.

**Type species.** *Nicon maculata* (Kinberg, 1866), designated by Pettibone, 1971.

**Diagnosis.** Prostomium subpyriform, with 2 pairs of eyes. Tentacular cirri with distinct cirrophores. Parapodia of first 2 setigers with notopodium represented by dorsal cirrus and single ligule. Dorsal cirri at bases of upper notopodial ligules. Subsequent notopodia with two ligules and small supra-acicular or presetal lobe between them. Neuropodia with conical or bilobed acicular lobes, digitiform or conical postsetal lobes, and lower ligules. Ventral cirri short, tapered. Notosetae homogomph spinigers only. Neurosetae homogomph and heterogomph spinigers, homogomph and heterogomph falcigers. Pharynx without papillae.

**Remarks.** The generic diagnosis taken from Pettibone (1971) has been expanded to include the presence of homogomph falcigers. This allows our new species of *Nicon*, *N. rotunda* to be included in the genus as in all other respects it agrees with Pettibone's expanded generic diagnosis.

As the neuropodial lobes of *Nicon* are not divisible into superior and inferior lobes as described in Fig. 1, the single neuropodial lobe is referred to as the acicular lobe in accordance with Pettibone (1971).

The genus *Nicon* was established by Kinberg (1866). He briefly described six new species, which were not figured and no type species for *Nicon* was designated. Hartman (1948) examined Kinberg's types, supplemented their descriptions and figured some of them. She selected *N. pictus* Kinberg as the type species without figuring it or giving a clear diagnosis. Pettibone (1971) in her revision of the genus designated *N. maculata* Kinberg as the type species, as this is the only species originally described by Kinberg (1866) sufficiently well preserved for an adequate diagnosis of the genus to be given. Of the 18 species, which were originally described as *Nicon*, or subsequently referred to it, only two species were retained in the genus by Pettibone (1971), including *N. maculata* Kinberg, 1866, and *N. aestuariensis* Knox, 1951. *Nicon abyssalis* Hartman, 1967 and *N. polaris* Hartman, 1967, have doubtful generic affinities (Pettibone, 1971).

*Nicon misakiensis* Imajima & Hayashi, 1969, was not considered by Pettibone in her revision. Subsequently, Wu & Sun, 1979 placed this species in the genus *Rullierinereis* Pettibone, 1971. We agree with the removal of this species from *Nicon*. *Rullierinereis misakiensis* has notopodial falcigers, a feature which can be used to distinguish the two genera as defined by Pettibone, 1971. Notopodial falcigers of *Nicon* are all spinigerous. Other species of *Nicon* described since Pettibone's (1971) revision include *N. japonicus* Imajima, 1972, *N. yaguinae* Fauchald, 1977 and *N. sinica* Wu & Sun, 1979.

This is the first time that the genus *Nicon* has been described from Australian waters.

### *Nicon maculata* Kinberg
Table 3

*Nicon maculata* Kinberg, 1866: 178.—Pettibone, 1971: 8–11, figs 1–2.—Wu & Sun, 1979: 101–102, fig. 4a–k.—Wu, *et al.*, 1985: 55–56, fig. 28a–k. See Pettibone, 1971 for synonomy.

**Material examined.** Australia: Tasmania: St Patricks Head 41°34.7'S 148°44.6'E, 109–1150m, 13 Dec. 1978, 1(AM W202509), 1(TASM K1095).

**Description.** Australian material posteriorly incomplete. 2 specimens, 29 mm long, 4 mm wide for 38 setigers and 50 mm long, 3 mm wide for 79 setigers were examined. Pharynx without papillae or paragnaths. Jaws amber coloured with approximately 14 rows teeth along cutting edges.

Anterior notopodia with cirriform dorsal cirri, bluntly conical dorsal and median ligules of approximately equal length, and small superior lobe. Dorsal cirri exceed notopodial ligules in length. Neuropodia with conical acicular and digitiform postsetal lobes, thick rounded to bullet-shaped lower neuropodial ligule and short, tapered ventral cirrus. Median and posterior parapodia with rami more widely separated. Dorsal cirri become more elongate posteriorly, notopodial and neuropodial lobes subconical to triangular rather than rounded. Neuropodial lobes and ventral ligule reduced in posterior setigers.

Notosetae with homogomph spinigers throughout. Neurosetae with homogomph spinigers and heterogomph falcigers. Heterogomph spinigers absent. Heterogomph falcigers long bladed anteriorly. Median and posterior parapodia, supra-acicular neuropodial falcigers with short, stout blades. Pygidium with long anal cirri.

**Remarks.** This species has been comprehensively described and illustrated by Pettibone (1971). Although we have not seen the type material, we are confident that the Australian material belongs to this species.

**Habitat.** Collected from 1090 to 1150 m. Substrate muddy sand. Pettibone (1971) gives the depth range of this species as 92 to 1153 m.

**Distribution.** Australia (Eastern Tasmania), East and South China Seas, Subantarctic and Antarctic waters. This is the first record of *Nicon maculata* from Australian waters.

### *Nicon moniloceras* (Hartman)
Fig. 2a–f, Tables 1 and 3

*Leptonereis glauca moniloceras* Hartman, 1940: 217, pl. 34, figs 42–46.

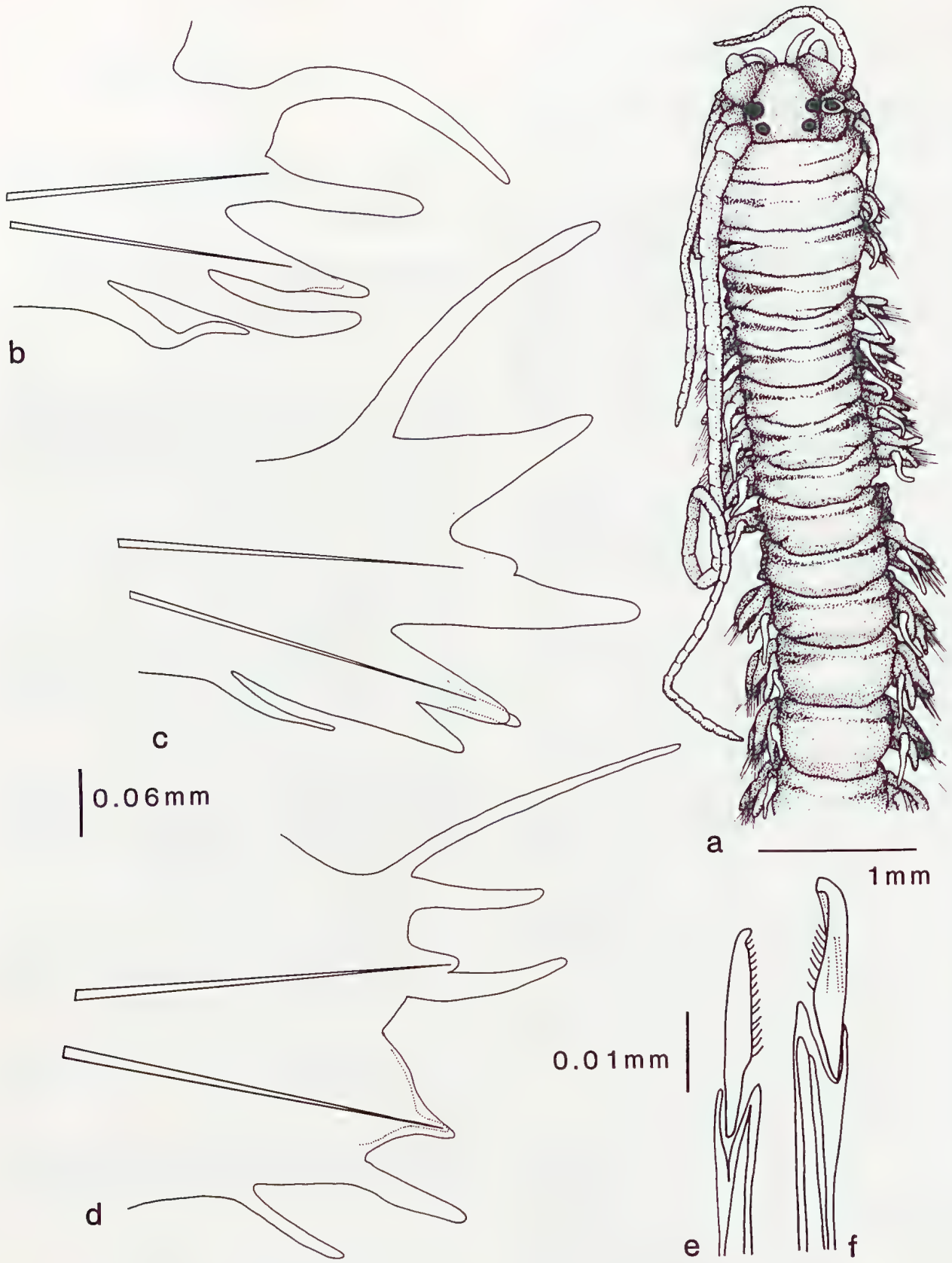


**Fig.2.** *Nicon moniloceras*: a, dorsal view of head end; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 50; e, heterogomph falciger parapodium 20; f, heterogomph falciger parapodium 50.

*Nicon moniloceras*.—Hartman, 1958: 265; 1959: 245, 274.—Imajima & Hartman, 1964: 150–151, pl. 35, figs a–c.—Imajima, 1972: 53–55, fig. 8.a–j.—Wu & Sun, 1979: 99, 101–104, fig. 5a–j.

**Material examined.** Australia: New South Wales: Wollongong 34°24'S, 151°19'E, 270-274 m, 13 Dec. 1978, 13(AM W202510), 10(AM W202511). HOLOTYPE: USA: California, Santa Catalina Island 33°24.35'N, 118°21.15'W, 72 m, 18 Nov. 1938, 1(AHF 0815); USA: California, Santa Catalina Island, 0.48 km east of Long Point 33°24.30'—33°24.15'N, 118°21.33'—118°21.35'W, 76-121 m, 25 June 1952, 1(AHF 2128-52); San Estaban Island, (south end) 28°39.40'N, 112°35.35'W, 27 Mar. 1937, 1(AHF 728-37); California, Baya, Ildefonso Island 26°37.20'N, 111°29.10NW, 90 m, 15 Mar. 1937, 1(AHF 677-37); California, Baja, Isabel Island 21°52.20'N, 105°51.35'W, 2 Apr. 1938, 1(AHF 748-37). Japan: Cape Shiriya-zaki, 41°24'N, 141°30'E, 140 m, Feb. 1956, 1(AHF N11091).

**Description.** Australian material, 13 specimens range from 0.5–1.0 mm wide. One specimen complete with 57 setigers. Gravid female with no sign of epitoky. Colour in alcohol pale brown with darker brown transverse bands on lateral, anterior edges of dorsum of anterior setigers (excluding apodous segment) after which bands very faint. Prostomial length slightly exceeds width. Eyes, large, black. Palps, stout with globular palpostyles, antennae approximately equal in length to prostomium (Fig. 2a). Tentacular cirri faintly annulated, longest extending to setiger 17. Jaws golden, translucent with 8 distinct teeth.

Setiger 3 (Fig. 2b) with single digitiform median notopodial ligule, from setiger 4 dorsal notopodial ligule present, approximately the same size and shape as median ligule. Between these, a smaller digitiform superior lobe (Fig. 2c). Posteriorly, dorsal and median ligules triangular, with dorsal ligule reduced in size in far posterior setigers.

Dorsal cirrus slightly longer than notopodial lobes throughout.

Neuropodia with blunt, triangular acicular lobe and slightly longer digitiform postsetal lobe (Fig. 2c). Ventral neuropodial ligule digitiform anteriorly, triangular posteriorly, slightly exceeds length of acicular lobe. Ventral cirrus narrow, tapering approximately two thirds length of neuropodium throughout.

Notosetae homogomph spinigers. Supra-acicular fascicle of neurosetae include homogomph spinigers and heterogomph falcigers. Subacicular fascicle of neurosetae include heterogomph spinigers and heterogomph falcigers. Falcigers with hooked distal tooth (Fig. 2e), increasingly hooked and with distinct tendon in far posterior setigers (Fig. 2f).

Pygidium with long anal cirri.

Setal counts for 10 specimens are shown in Table 1.

**Remarks.** The Australian material agrees well with the descriptions of Hartman (1940) and Imajima (1972). Pettibone (1971) examined the holotype, a single female heteronereid dredged from 37 m off Catalina Island, Southern California (AHF 0815). She tentatively assigned the species to *Platynereis* because of the presence of long tentacular cirri and setae. She suggests that the shape of the prostomium is more like *Platynereis* than *Nicon* and suggests that the minute paragnaths may have been overlooked. The holotype is in very good condition and in our opinion is correctly assigned to the genus *Nicon*. No paragnaths or traces of paragnaths can be detected in the holotype or additional material examined from California or Japan. Although paragnaths are often absorbed in heteronereids, in our experience this is usually only partial and generally in such specimens some traces of paragnaths can be seen. Long tentacular cirri, particularly the dorsalmost pair are characteristic in this species. Other diagnostic characters are shown in Table 3. The species is well figured and described by Imajima (1972).

**Habitat.** Australian material occurring in thick fibrous tubes with attached sand grains, at 270 to 274 m. Holotype collected at 72 m in habitat of rock, brachiopods and sponges. Other material examined collected between 75 to 140 m, sand, gravel and amongst *Laqueus* shells.

**Distribution.** Eastern Australia, California south to western Mexico, China, northern Japan.

### *Nicon rotunda* n.sp.

Fig. 3a–g, Tables 2, 3

**Material examined.** HOLOTYPE: Australia: Northern Territory: Port Darwin 12°27'S, 130°50'E, subtidal, 6 Mar. 1965, 1(AM W202512), 50 mm long, 3.5 mm wide, 92 setigers, complete. PARATYPES: Northern Territory, Port Darwin 12°27'S, 130°50'E, subtidal, 6 Mar. 1965, 1(AM W202513). New South Wales: Newcastle 33°06.2'S, 156°09.3'E, 154-164 m, 7 Oct. 1982, 1(AM W202514), 1(AHF POLY 1490), 1(BMNH ZB 1988.14), (USNM 120509), (NMV F57446). Paratypes range from 0.75-1.25 mm wide. 2 specimens complete, the largest 1(AHF POLY 1490), 18 mm long, 0.75 mm wide, 70 setigers.

**Description.** Preserved animal, pale yellow in colour. Pale brown glands visible on dorsal surface of dorsal notopodial ligule and at base of dorsal cirri posteriorly. Paired brown blotches on either side of posterior ventrum. Holotype a gravid male with enlarged eyes, but no other signs of epitoky.

Prostomium elongate, trapezoidal, with blunt anterior margin, and prominent dorsal furrow. Eyes coalesced, present on lateral margins of prostomium. Palps with globular palpophores and small rounded palpostyles. Tentacular cirri indistinctly annulated, longest extending to setiger 2. Fine jaws, not heavily sclerotised, translucent, pale golden with 9 teeth along the cutting margin (Fig. 3a). Setiger 1 with broad-based, dorsal cirri extending beyond bluntly conical, dorsal notopodial ligule. Neuropodia with narrow, triangular, acicular lobe and slightly longer, triangular, postsetal lobe. Neuropodial ligule thick and rounded, slightly longer than notopodial ligule. Ventral

cirri broad, tapering, and slightly shorter than neuropodial ligule. Parapodia 3, 10 and 20 (Fig. 3b–d) with dorsal and ventral cirri as described for setiger 1. Both cirri persist in similar proportions posteriorly but become proportionally narrower from about setiger 20. Anterior notopodia with widely separated, dorsal and median ligules with digitiform superior lobe. Both dorsal and median ligules conical in shape in anterior setigers, becoming triangular in posterior setigers (Fig. 3d,e). Dorsal notopodial ligule slightly exceeds median ligule in size in all parapodia.

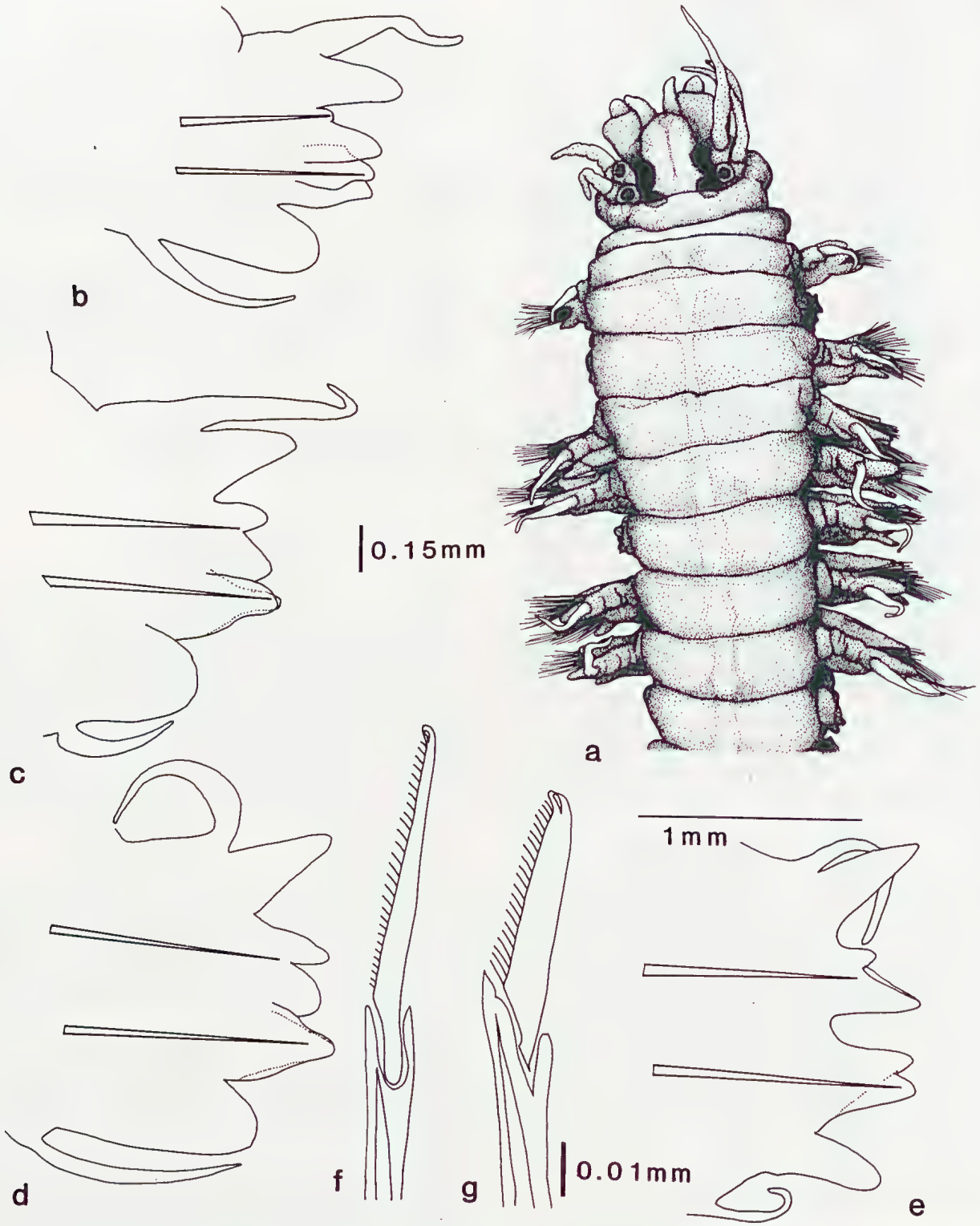


**Fig.3.** *Nicon rotunda* n.sp., holotype (AM W202513): a, dorsal view of head end; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 20; e, anterior view of parapodium 50; f, homogomph falciger, subacicular fascicle, parapodium 10; g, heterogomph falciger, subacicular fascicle, parapodium 20.

Anterior neuropodia with bluntly, triangular, acicular and postsetal lobes which become, after the first few setigers, approximately equal in length. Posteriorly, neuropodial lobes pointed. Ventral neuropodial ligules, on anterior parapodia, broad and conical, becoming narrower posteriorly and in far posterior setigers triangular in shape. Relative size of this ligule, which is approximately two thirds as long as postsetal and acicular lobes, remains constant in all setigers.

Notosetae all homogomph spinigers. Neuropodial supra-acicular fascicle with homogomph spinigers and heterogomph falcigers. Neuropodial subacicular fascicle with homogomph spinigers, and heterogomph falcigers throughout and homogomph falcigers in dorsal region of subacicular fascicle of anterior parapodia only. Homogomph falcigers with long, narrow blades (Fig. 3f), heterogomph falcigers, also long-bladed with hooked distal tooth, more obviously so in posterior setigers (Fig. 3g).

Pygidium with delicate anal cirri, 1 mm in length.

The number and distribution of setal types for the holotype and paratypes are shown in Table 2.

**Remarks.** The paratypes exhibit some variation in setal counts compared to the holotype as shown in Table 2, however in other characters, paratypes resemble the holotype closely. *Nicon rotunda* n.sp. can be distinguished from the other described species of *Nicon*, using the characters shown in Table 3.

*Nicon rotunda* resembles *N. maculata* in the overall structure of the parapodia, particularly with respect to the distinctive thick, rounded, ventral neuropodial ligules present in both species. However, the presence of subacicular neuropodial homogomph falcigers in *Nicon rotunda* can be used to distinguish this species from the two other species of *Nicon* recorded from Australia, *N. maculata* and *N. moniloceras*.

The material from Northern Territory was collected intertidally whereas that from New South Wales was collected from 154 to 164 m. Material from the two localities is morphologically identical and although the habitats are very different we cannot morphologically distinguish between the individuals from these two localities. Limited collecting has been done in shallow subtidal areas between Darwin and NSW and the species may have a more continuous distribution than currently indicated.

**Habitat.** Specimens from near Darwin were collected intertidally and those from New South Wales from 154 to 164m.

**Distribution.** Australia (Northern Territory, New South Wales).

**Etymology.** The specific name is the Latin *rotundus* and refers to the rounded, ventral neuropodial ligules present in this species.

### *Australonereis* Hartman

*Australonereis* Hartman, 1954: 19.

**Type species.** *Australonereis ehlersi* (Augener, 1913), designated by Hartman, 1954.

**Diagnosis.** Eversible pharynx with papillae on maxillary ring, oral ring bare. Papillae sometimes with horny tips. Notosetae homogomph spinigers, neurosetae homo- and heterogomph falcigers. Fleshy transverse ridges present on anterior ventrum.

**Remarks.** The presence of horny tips on the pharyngeal papillae is reported for the first time, and included in the generic diagnosis. The genus is known only from Australia.

### *Australonereis ehlersi* (Augener)
Fig. 4

*Nereis (Leonnates) ehlersi* Augener, 1913: 142–145, fig. 12a–c, pl. 3 fig. 53.
*Leonnates ehlersi*.—Monro, 1938: 618-623, fig. 7–13.
*Australonereis ehlersi*.—Hartman, 1954: 19–23, figs 1–11.—Hutchings & Rainer, 1979: 752–753.—Hutchings & Turvey, 1982: 96–97.—Hutchings & Murray, 1984: 36.

**Material examined.** Australia: Western Australia: Bunbury, Leschenault Estuary 33°16'S, 115°42'E, 24 June 1965, 1(AM W6813); Swan River 31°45'S, 116°04'E, 24 Mar. 1987, 6(AM W202496). Queensland: Gladstone, Calliope River 23°55'S, 151°10'E, 1974, 4(AM W199374); Frazer Island, Moon Creek 25°22'S, 153°07'E, 30 Dec. 1971, 2(AM W5375); Hervey Bay, Kangaroo Island 25°26'S,152°53'E, 29 Dec. 1971, 4(AM W5374); Cribb Island, Jackson Creek 27°21'S, 153°07'E, 12(QM G7571); Moreton Bay, Lytton 27°25'S,153°20'E, 2(QM G7129). New South Wales: Myall River 32°18'S,

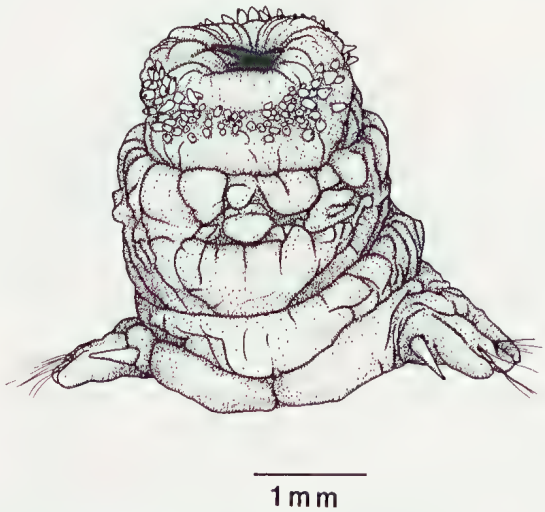


**Fig. 4.** *Australonereis ehlersi*: ventral view head end showing everted proboscis with horny tipped papillae.

152°11'E, 9 Feb. 1974, 1(AM W6121); Ettalong Beach 33°31'S,151°19'E, 13 Apr. 1946, 10(AM W3487); Hawkesbury River 33°30'S, 151°10'E, 31 Aug. 1982, 1(AM W9082); Botany Bay, Towra Point 34°00'S, 151°11'E, 4 June 1977, 1(AM W12304); Merimbula Lake 36°54'S, 149°53'E, 17 Mar. 1976, 1(AM W12168). Victoria: Mallacoota Inlet, Gravelly Point 37°34'S, 149°46'E, 18 Feb. 1973, 5(AM W8444); Gippsland Lakes 37°53'S, 148°00'E, many (AM W5514); Inverloch, Venus Bay 38°38'S, 145°44'E, 12 Oct. 1980, 4(AM W18595); Glenelg River 37°17'S, 141°16'E, 17 June 1975, 3(AM W9192). Tasmania: Midway Point 42°48'S, 147°32'E, 9 Dec. 1973, 1(TASM K966). South Australia: The Coorong 35°59'S, 139°31'E, 28 July 1974, 3(AM W8426); Torrens Island 34°47'S, 138°32'E, 11 Jan. 1974, 5(AM W6773); Adelaide, St Vincent Gulf 34°45'S, 137°57'E, 1(SAM E2355); Onkaparinga Estuary 35°00'S, 138°49'E. 1973, many (AM W6061).

A selection of material examined. All specimens collected intertidally.

**Description.** Material examined range up to 140 mm long and 12 mm wide. Colour in alcohol variable cream-pink, rust-brown, olive green. Often with brown blotches on dorsum of head and first few setigers. In life, animals green-red with anterior setigers darker. Body flattened particularly in median and posterior regions. Pharynx with oral ring smooth, maxillary ring with more than 50 (sometimes in excess of 100) short cirrus-like papillae, with or without horny tips (Fig. 4). Papillae most numerous midventrally, fewest laterally. Papillae larger dorsally than ventrally, anteriormost longer than those on posterior margin. Anterior parapodia and ventrum from approximately setiger 7 to setiger 30 with thickened lobes and thick, glandular transverse ridges (maximum 7–8). Following setigers without such papillae.

Anterior notopodia with short, cirriform dorsal cirri, triangular dorsal and median ligules and small, rounded superior lobe. Anterior neuropodia with rectangular acicular lobe, a bluntly rounded postsetal lobe and a small, cirriform ventral ligule, and ventral cirrus. Median and posterior parapodia, notopodial lobes elongate, exceeding neuropodial lobes in length. Dorsal ligule exceeds length of median ligule, superior lobe greatly reduced. Neuropodia, ventral ligule increases in size posteriorly to approximate size of acicular lobe.

In median to posterior setigers, coelomostomes present as large lobes arising from proximal base of dorsal cirrus.

Setae most numerous anteriorly. Notopodia with homogomph spinigers. Neuropodia with homogomph and sesquigomph spinigers and sesquigomph falcigers. Falcigers terminate in a hooked process which usually overlaps last few distal teeth. Teeth long slightly curved. Falcigers well figured by Hartman (1954).

**Remarks.** This is the first time that *Australonereis ehlersi* has been reported as having brown horny tips on the pharyngeal papillae. These horny tipped papillae do not occur on all specimens, and animals with and without horny tipped papillae have been found (a) over the entire range of the species, (b) within the same locality and specimen lot, (c) in specimens of different size ranges, (d) in specimens of both sexes, (e) within material from the type locality, the Swan River. In some individuals the papillae appear to have darkened or shiny tips but they are not fully sclerotised. It appears therefore that the species may or may not possess papillae with horny tips and this is unrelated to size, maturity, sex or locality. We have therefore expanded the species description and the generic diagnosis.

Hartman (1954) reported coelomostomes to occur only in ovigerous specimens, however they also occur in mature males.

This species is well represented in collections from southern and south-eastern Australia. The northernmost extent of its range on the east coast is Gladstone, Queensland, 23°55'S, 151°10'E and on the west coast, specimens have been collected only as far north as the type locality, Swan River, 31°45'S, 116°04'E.

**Habitat.** Lives in muddy sand and sand flats consisting of fine coarse grained sediment, in angular, flimsy, sandy tubes, which protrude slightly above the surface. Often associated with *Posidonia, Halophila, Zostera* seagrass beds and *Rhizophora* mangroves.

**Distribution.** Australia (Gladstone, Qld to Bunbury, W.A.).

## *Dendronereides* Southern

*Dendronereides* Southern, 1921: 602-603.—Day, 1967: 302.

**Type species.** *Dendronereides heteropoda* Southern, 1921, by original designation.

**Diagnosis.** Pharynx with soft papillae on oral and maxillary rings. In the anterior region, the dorsal notopodial lobe of the notopodium is divided to form a simple series of branchial filaments. Inferior lobe of neuropodium absent. Parapodial lobes reduced and simplified posteriorly.

### *Dendronereides heteropoda* Southern
Fig. 5a, Table 4

*Dendronereides heteropoda* Southern, 1921: 603–607, fig. 10a–f, pl. 21 fig. 6A–N.—Hanley, 1985: 244 (in part, rest = *D. zululandica* Day).

**Material examined.** Australia: Northern Territory: Daly River 13°55'S, 130°56'E, 15 Aug. 1985, 1(NTM W2015), 9 Jan. 1985, 1(NTM W2748); Browns Creek 13°41'S, 130°40'E, 8 Jan. 1985, 1(NTM W2741), 1(NTM W2743), 1(NTM W2744), 1(NTM W2745), 1(NTM W2746); Palmerston Island 13°21'S, 130°19'E, 15 Aug. 1984, 1(NTM W2012), 9(NTM W2013), 1(NTM W2014), 1(NTM W2016); Wollianna Station 13°39'S,

130°39'E, 5 Jan. 1985, 1(NTM W2467), 1(NTM W2711), 6 Jan. 1985, 1(NTM W2725), 1(NTM W2727), 1(NTM W2728), 1(NTM W2729), 1(NTM W2730), 1(NTM W2731), 1(NTM W2732), 1(NTM W2734), 1(NTM W2735), 1(NTM W2738), 1(NTM W2739); McArthur River, Carrington Channel 15°50'S, 136°35'E, 8 Aug. 1985, 1(NTM W3717), Curie Channel, 7 Aug. 1985, 1(NTM W3088), 1(NTM W3099), 1(NTM W3102), 1(NTM W3104), 1(NTM W3105), 1(NTM 3106), 1(NTM W3108), 1(NTM W3109), 1(NTM W3113), 1(NTM W3167), 1(NTM W3175), 1(NTM W3176), 1(NTM W3178), 1(NTM W3499), 1(NTM W3501).

A selection of material examined. All specimens collected intertidally.

**Description.** Smallest specimen 7 mm long, 0.5 mm wide for 39 setigers, posteriorly complete. Largest specimen, posteriorly incomplete, 52 mm long, 3.0 mm wide, 122 setigers. Prostomium with deep median furrow. Jaws with many fine teeth (10–20). Pharynx with papillae arranged as follows: Area I–IV, a band of fine, pointed papillae, 4–5 deep with those on dorso-lateral edge of the maxillary ring longer than those in dorsal and lateral positions. Area V = 3–4, VI = 3–4, VII–VIII = a band in 2–4 rows.

Anterior parapodia, notopodia from setiger 3 with short, stout subconical dorsal cirri, triangular-subconical dorsal ligules and slightly longer median ligules. Superior lobes present as a low rounded fillet, lying anterior to the median ligule. Neuropodia with 3 digitiform lobes, 2 acicular and 1 postacicular lobe. Ventral cirrus short, blunt subconical. Median and posterior parapodia, notopodial dorsal ligule divided forming branchiae which begin on setiger 6 or 7 and continue to setiger 29 or 30. Branchial filaments fine, feathery, branch in all directions from a basal point (Fig. 5a).

Remaining lobes as for anterior parapodia with notopodial median ligule increasing in size posteriorly. Neuropodial lobes decrease in size posteriorly, with ventral acicular lobe absent in far posterior setigers. Branchial filaments decrease in number posteriorly until in far posterior setigers, no dorsal ligule present.

Setae consist of homogomph spinigers, sesquigomph spinigers and homogomph falcigers. Posteriorly, supra-acicular neuropodial spinigers heavily chitinised.

The number of setal types found along the body for a number of individuals are shown in Table 4. Setal types homogomph and sesquigomph have been grouped together, as, when setae are dense and overlapping as seen in the neuropodia, shaft type is difficult to ascertain.

**Remarks.** Some of the material from Wollianna station, Daly River, (NTM W2739), (NTM W2730), (NTM W2467), (NTM W2734) has fewer branchial filaments than other material examined, however it agrees well in other respects to the description given by Southern (1921). The number of branchial filaments appears to be related to size, smaller specimens having fewer filaments per setiger. The specimen described by Southern (1921) which was 66mm long, had a maximum development of branchiae on setiger 21 with 60–75 filaments. Our largest specimen also has approximately 60 filaments on setiger 21.

*Dendronereides heteropoda* has previously been recorded from northern Australia by Hanley (1985). Re-examination of this material showed that two species had been confused, *Dendronereides zululandica* Day, 1951 and *D. heteropoda*. The two species have overlapping geographical distributions. *Dendronereides heteropoda* can be separated from *D. zululandica* by the arrangement

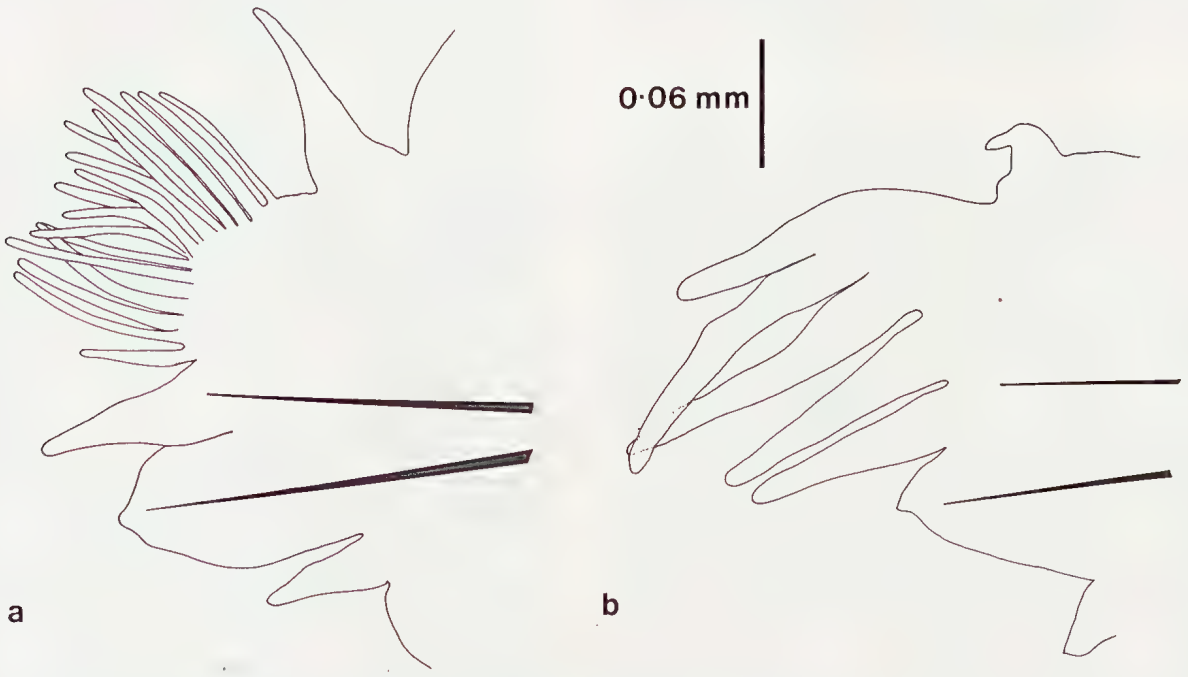


**Fig.5.** *Dendronereides heteropoda* (NTM W2013): a, parapodium 25. *Dendronereides zululandica* (NTM W2060): b, parapodium 25.

of the papillae on the pharynx, shape of the branchiae and setal types. Heterogomph spinigers and falcigers seen in *D. zululandica* are not present in *D. heteropoda*. Some differences in setal form occur within these two species, the heavily chitinised sesquigomph spinigers present posteriorly in *D. heteropoda* are absent in *D. zululandica*.

Storch & Welsch (1972) collected *D. heteropoda* in mangrove swamps of Belawan, Sumatra for a physiological study.

**Habitat.** In Australia, the species occurs on mud flats seaward of mangroves *Avicennia marina* and *Rhizophora*. Southern (1921) describes the habitat as brackish pools and salt lakes with variable, but never high salinity.

**Distribution.** Australia (Northern Territory). India (Barantolla), Sumatra (Belawan).

### *Dendronereides zululandica* Day
Fig. 5b, Table 5

*Dendronereides zululandica* Day, 1951: 30–32, fig. 5a–j.—Day, 1967: 302–304, fig. 14.3 g–l.

**Material examined.** Australia: Western Australia: King River, Wyndam 15°47'S, 128°12'E, 21 Mar. 1985, 1(NTM W2618), 23 Mar. 1985, 1(NTM W2623), 21 Mar. 1985, 1(NTM W2628), 21 Mar. 1985, 1(NTM W2629). Northern Territory: Micketts Creek, Shoal Bay 11°48'S, 130°39'E, 21 June 1982, 2(NTM W2060); Gunn Point 12°10'S, 131°00'E, 3 Oct. 1981, 3(NTM W210); McArthur River; Carrington Channel 15°50'S, 136°35'E, 8 Aug. 1985, 1(NTM W3721); Cora Point, 3 Aug. 1985, 1(NTM W3120), 3 Aug. 1985, 1(NTM W3425); Muggs Mistake 15°55'S, 136°36'E, 1 Aug. 1985, 1(NTM W3738). HOLOTYPE: South Africa, Zululand, St Lucia Estuary, 28°32'S, 32°25'E (BMNH 5.5.1/28).

**Description.** All material examined posteriorly incomplete, ranging from 6.0–20 mm long, 0.5–2.0 mm wide, 39–68 setigers. Prostomium semicircular with median furrow. Pharynx with papillae arranged as follows: Areas I–IV=26–44, V=1 large papilla, VI=1–2 papillae (if 2 papillae present one small), VII–VIII=6–12 in 2 alternating rows with largest papillae occurring toward maxillary end of oral ring.

Anterior notopodia with short, pointed dorsal cirrus, triangular dorsal and median ligules. Superior lobe present after first few setigers. From approximately setigers 7–30, dorsal ligule divided to form long, fingerlike branchiae (Fig. 5b). Branchiae project in a plane approximately parallel to parapodia. Neuropodia with single, broad, rounded lobe not divided into separate acicular and post acicular portions. Ventral cirrus short, pointed. Posteriorly, notopodial lobes reduced in number to 2 then 1 lobe. Neuropodia a single conical lobe.

Setae consist of homogomph and heterogomph spinigers and homogomph and heterogomph falcigers. The variation in the distribution of setae along the body is given in Table 5.

**Remarks.** The Australian material closely resembles the type of *D. zululandica*. This represents the first record of *D. zululandica* from outside South Africa. The specimens in northern Australia were found in a similar estuarine habitat to that of the type locality.

The two species of *Dendronereides* found in Australia occur together in the McArthur River (Carrington Channel). *Dendronereides heteropoda* has also been collected from Port Essington and the Daly River but to date no *D. zululandica* have been collected from these more westward localities.

**Habitat.** In Australia the species occurs on mud flats in front of mangroves (*Avicennia marina* and *Rhizophora* sp.). Day, (1967) records specimens occurring in tropical estuaries.

**Distribution.** Australia (Western Australia, Northern Territory), South Africa.

### *Ceratophale* Malmgren

*Ceratophale* Malmgren, 1867: 176–177.—Hartman, 1952: 15–16.—Banse, 1977: 613–614. See Banse, 1977 for synonymy.—Hylleberg & Nateewathana, 1988: 5.

**Type species.** *Ceratocephale loveni* Malmgren, 1867 by original designation.

**Diagnosis.** Pharynx with papillae on oral ring. Dorsal cirri simple throughout. Median body region with dorsal cirri on elongated vascularised cirrophores, with or without mid-dorsal transverse flaps and with conspicuous neuropodial presetal ligules.

**Remarks.** We have partially adopted the terminology used by Hylleberg & Nateewathana (1988) to describe the complex parapodia of *Ceratocephale* and *Gymnonereis*.

Notopodia and neuropodia consist of presetal ligules and postsetal lobes. The acicula are embedded in the noto- and neuro-acicular papillae respectively.

We have retained the term ventral ligule to describe the ligule immediately ventral to the neuropodial presetal ligule and postsetal lobe. Ventral cirri are described as bifid, with the dorsalmost cirrus of the pair called the primary cirrus (after Banse, 1977).

Hylleberg & Nateewathana (1988) and Pettibone (1970) refer to the ventral ligule, as a subpodal ligule, retaining the term ventral ligule for the primary ventral cirrus.

It is difficult to decide whether the bifid ventral cirri of *Ceratocephale* are homologous with the single ventral cirri of other nereidids (ie. bifidness is a state of the character ventral cirri-form), or whether the dorsalmost one of the pair is homologous with the ventral ligule of other nereidids. Therefore, by following the terminology of Banse, 1977 in describing the ventral cirri as bifid we are not necessarily implying homology.

***Ceratocephale aureola* n.sp.**
Fig. 6a–f, Tables 6, 9

**Material examined.** HOLOTYPE: Australia: Western Australia: Dampier Archipelago, Enderby Island 20°36'S, 116°30'E, 3 Mar. 1987, 1(AM W202515) 13 mm long, 0.75 mm wide, 62 setigers, posteriorly incomplete. Collected intertidally.

**Description.** Alcohol preserved worm pale brown in colour with no pigment patterns, parapodia with prominent dark brown acicula and golden brown setae. Setae more abundant on anterior 10 setigers compared with subsequent setigers.

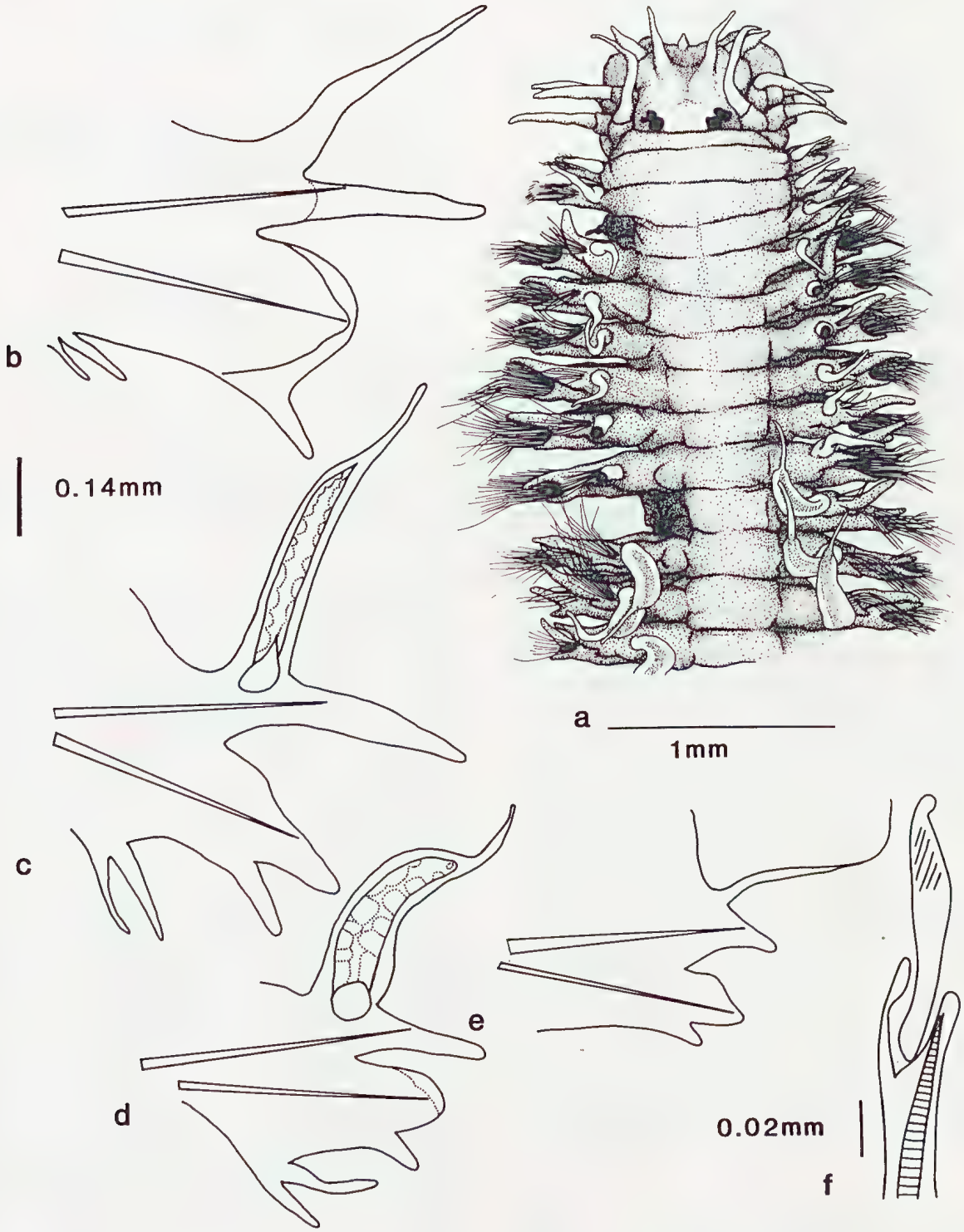


**Fig.6.** *Ceratocephale aureola* n.sp., holotype (AM W202515): a, dorsal view of head end; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 20; e, anterior view parapodium 50; f, sesquigomph falciger, parapodium 3.

Prostomium narrow, rectangular with a pair of widely spaced, biarticulate antennae. Antennae with elongate, globular ceratophores and narrow, elongate ceratostyles, both components similar in length. Palps situated on extreme lateral margins of prostomium, palpophores globular and fused laterally to antennae, palpostyles triangular, similar in length but thicker than ceratostyles of antennae. Eyes black, arranged diagonally at the base of prostomium. Anterior pair of eyes kidney-shaped and posterior pair almost spherical in shape (Fig. 6a).

Peristomium narrow, tentacular cirri of equal length, extending to setiger 2. Pharynx with pair of light brown, poorly sclerotised jaws with 8 teeth. Basal ring with elongate, colourless papillae arranged as follows: Area V=1, VI=1, VII-VIII=7.

Dorsal cirri initially small, narrow, triangular lobe, gradually increasing in size and by setiger 10, dorsal cirri elongated and expanded with a distinctive terminal flag (Fig. 6c). Dorsal cirri approximately 1.5 times as long as parapodial lobes along entire length of animal. Ventral cirri unequally bifid from setiger 1. Primary cirri longest with ventralmost cirri increasing in length over first 10 setigers to approximate length of primary cirri. Posteriorly, ventralmost cirri decreases in length.

Setiger 1, neuropodia with triangular postsetal lobe, digitiform neuro-acicular papilla, elongate presetal ligule which slightly exceeds postsetal lobe in length. Ventral ligule triangular, shorter than superior lobe.

Setiger 3 (Fig. 6b), notopodial presetal ligule triangular, with short, rounded postsetal lobe. Notopodial lobes twice as long as neuropodial lobes. Neuropodia with very small, neuro-acicular papilla, conical presetal ligule and slightly longer, rounded postsetal lobe and blunt, triangular ventral ligule.

Setiger 10 (Fig. 6c), with vascularised, expanded dorsal cirrus. Notopodia, as for setiger 3 with notopodial presetal ligule approximately 1.5 times as long as neuropodial lobes. Neuropodia small, pointed, superior neuro-acicular papilla, elongate, triangular presetal ligule and longer, rounded postsetal lobe. Ventral ligule triangular.

Setiger 50 (Fig. 6e), presetal notopodial ligule elongate. Neuropodia with broad, triangular postsetal lobe and shorter, rounded presetal ligule, plus small, blunt, triangular ventral ligule.

Parapodia decrease in size posteriorly from setiger 20.

Setae consist of homogomph spinigers, sesquigomph spinigers and sesquigomph falcigers in far anterior neuropodia.

Setal counts for selected parapodia of the holotype are shown in Table 6.

Body wall ventrally smooth, dorsally with distinct transverse ridges connecting parapodia; ridges most prominent on setigers 10–25, then ridges gradually disappear. Gut full of calcareous sand. Holotype not gravid.

**Remarks.** *Ceratocephale aureola* n.sp. can be separated from *Ceratocephale setosa* n.sp. as the latter has bifid ventral cirri from setiger 3. Setae of *C. ?pacifica* are all spinigers whereas *C. aureola* and *C. setosa* have sesquigomph falcigers in anterior setigers. In Table 9, the diagnostic characters which separate *Ceratocephale aureola* from other species of *Ceratocephale* are given. Although only a single specimen of this new species was collected, we felt justified in describing it as a new species, as it clearly differs from all other described species of the genus (Table 9).

**Habitat.** The single specimen was found on an intertidal mud flat in front of mangroves.

**Distribution.** Australia (Western Australia).

**Etymology.** The specific name aureola refers to the golden setae occurring in this species, and is derived from the Latin *aureolus*, meaning golden.

### *Ceratocephale ?pacifica* Hartman

Fig. 7a–e, Tables 7, 9

*Ceratocephale loveni pacifica* Hartman, 1960: 94–96, pl. 8, figs 1,2.

*Ceratocephale pacifica* Banse, 1977: 617, fig. 2a. (in part)

**Material examined.** Australia: Victoria, Bass Strait 38°27.8'S, 148°53.6'E, 2350 m, 15 Nov. 1981 1(NMV F50060). Bass Strait 38°24.5'S, 148°42.1'E, 1200 m, 15 Nov. 1988, 1(NMV F50059).

**Description.** 2 specimens posteriorly incomplete, 2.0 and 6.0 mm long, 0.4 mm and 1.0 mm wide, with 14 and 23 setigers respectively. Alcohol preserved material, pale cream in colour with golden setae and dark brown aciculae slightly emergent. Prostomium rectangular and bulbous, with pair of long, thin, triangular antennae lying closely against palps. Globular palps with triangular palpophores. Eyes absent. Tentacular cirri with longest extending to setiger 1 (Fig. 7a).

Pharynx with a pair of pale brown, sclerotised jaws with about 8 teeth, papillae absent.

Setiger 1 with narrow, bifid ventral cirrus, ventralmost branch half length of primary branch. Neuropodia with triangular postsetal lobe and slightly longer, triangular presetal ligule. Ventral neuropodial ligule, short, digitiform, half length of primary ventral cirrus. Dorsal cirrus fine tapering, longer than neuropodial ligules. Subsequently, dorsal cirri expand in width and length with apex of cirri drawn out forming finely tapered tip. Fully expanded vascularised dorsal cirri present from setiger 8. Notopodia with elongate, triangular presetal ligule and very short, blunt postsetal lobe. Neuropodia with bluntly, triangular postsetal lobe and very short, neuro-acicular papilla and digitiform presetal ligule which exceeds length of postsetal lobe. Ventral neuropodial ligule short, triangular (Fig. 7b). Ventral cirri bifid throughout, with ventralmost cirri slender to setiger 5, subsequently broad, globular at base and half to two thirds as long as slender primary cirri (Fig. 7d).

Notopodial setae arranged in 2 bundles on either side of

presetal ligule. Neuropodial setae similarly arranged.

Setae consist of homogomph and sesquigomph spinigers with finely serrated blades (Fig. 7e). The number of sesquigomph spinigers present per parapodia increases along length of animal. Number of homogomph spinigers per parapodium increases to setiger 10, subsequently decreases and by setiger 20, only sesquigomph spinigers present in neuropodia. Table 7 shows setal counts for specimens (NMV F50060). Setae far more numerous on setigers 3–9 than on subsequent setigers. Setae straw coloured. Narrow transverse dorsal ridges connecting the parapodia present on setigers 10–19.

Specimen (NMV F50060) gravid with no sign of epitokal modifications.

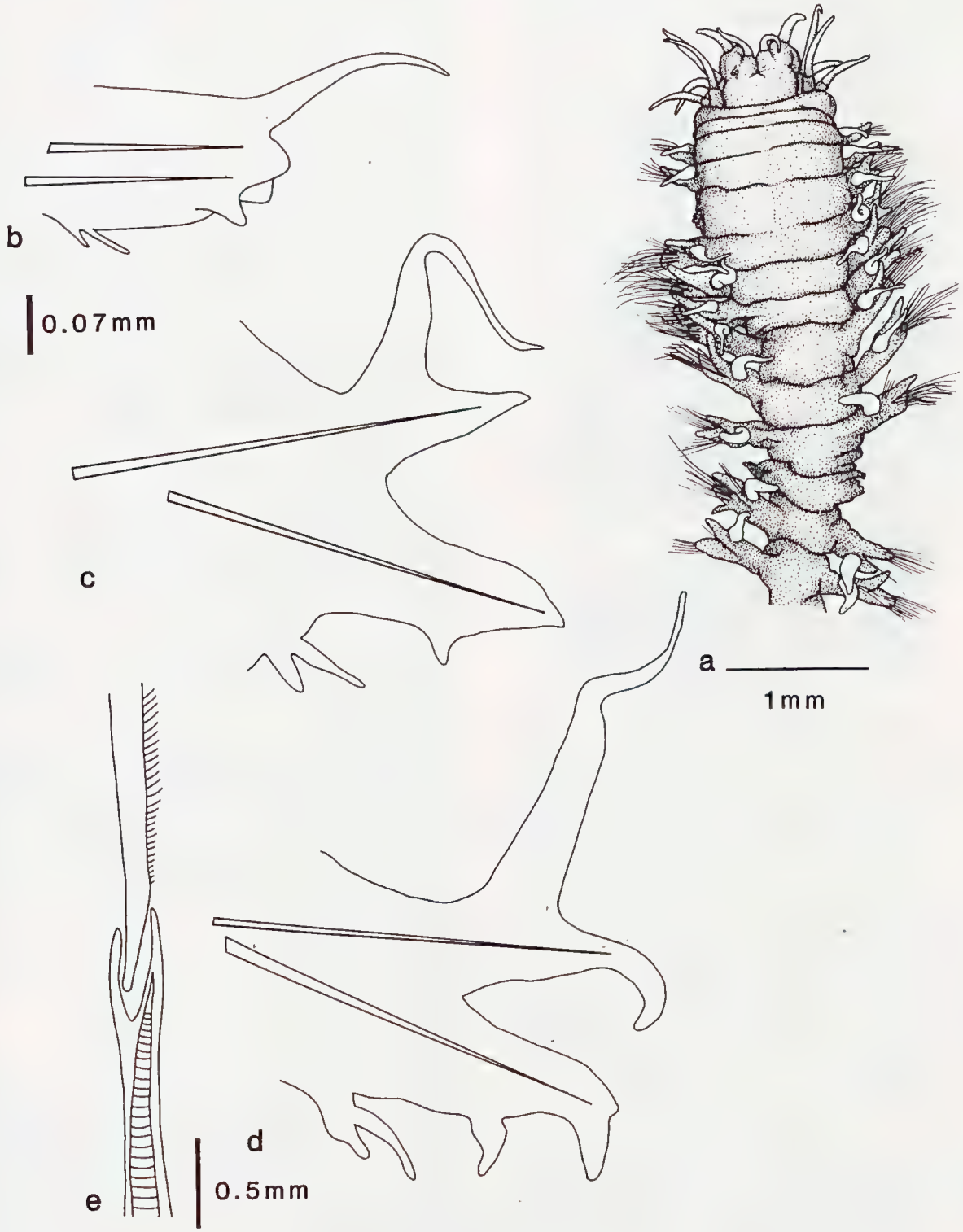


**Fig.7.** *Ceratocephale ?pacifica* (NMV F50059): a, anterior end, dorsal view; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 20; e, sesquigomph spiniger (part) parapodium 20.

**Remarks.** This species closely resembles *Ceratocephale pacifica* as described originally by Hartman (1960) as *C. loveni pacifica* and subsequently re-examined by Banse (1977). Banse elevated the subspecies to the species level and indicates that two species were confused by Hartman (1960) and that not all specimens designated as type material belong to *C. pacifica*, the remainder belonging to a second species *C. hartmanae* Banse, 1977. Thus in Table 9 we have listed the characters as outlined by Banse (1977) for *C. pacifica*. Hartman describes dorsal ridges as present from setiger 8, however they appear to start from setiger 10 in our material. As we have seen only two small specimens of this species and have not examined the type material, we have tentatively assigned them to *Ceratocephale ?pacifica* until more material becomes available. Table 9 shows a comparison of selected characters of the seven described species of *Ceratocephale*. *Ceratocephale ?pacifica* and *C. aureola* n.sp. both have bifid ventral cirri from setiger 1, however the latter can be distinguished from *C. ?pacifica* by the presence of sesquigomph falcigers. *Ceratophale setosa* has bifid ventral cirri from setiger 3. No papillae could be seen in *C. ?pacifica*, however both specimens are extremely small and the head of one specimen is dorsoventrally flattened making detection of papillae difficult.

**Habitat.** The Australian material was collected from depths of 1200 to 2350 m, in mud. The type of *C. pacifica* was collected from depths of over 1800 m, in the West Cortes Basin off Southern California, USA also in mud.

**Distribution.** Australia (Victoria).

### *Ceratocephale setosa* n.sp.
Fig. 8a–e, Tables 8, 9

**Material examined.** HOLOTYPE: Australia: Victoria: Port Phillip Bay 38°18.7'S, 144°53.3'E, 18 m, 10 Feb. 1970, 1(AM W16093) 15 mm long, 1.5 mm wide, 54 setigers, incomplete posteriorly. PARATYPES: Victoria: Port Phillip Bay 38°18.7'S, 144°42.9'E, 18 m, 10 Feb. 1970, 1(NMV F54174), 11 mm long, 1.5 mm wide, 24 setigers; Port Phillip Bay 38°04.7'S, 144°42.9'E, 15 m, 10 Feb. 1970, 1(AHF POLY 1489), 10 mm long, 1.0 mm wide, 36 setigers; Port Phillip Bay 38°04.7'S, 144°42.9'E, 15 m, 10 Feb. 1970, 1(BMNH ZB 1988.13), 10 mm long, 0.9 mm wide, 30 setigers; Port Phillip Bay 38°04.7'S, 144°42.9'E, 15 m, 10 Feb. 1970, 1(USNM 120512), 7 mm long, 1.0 mm wide, 29 setigers. All paratypes posteriorly incomplete. Non-type material: Victoria: Port Phillip Bay, 38°04.7'S, 144°42.9'E, 15 m, 10 Feb. 1970, 3(AM W16092). South Australia: Upper Spencer Gulf 33°24'S, 137°37'E, 9.3 m, Apr. 1979, 1(AM W202508).

**Description.** Alcohol preserved worm pale cream in colour, with pale golden setae. Anterior 12 segments inflated, body then tapers and all subsequent segments similar in width. Anterior setigers with numerous setae, following setigers with fewer setae.

Prostomium, oblong with two pairs of eyes on basal, lateral margins, arranged in an oblique line. Basal pair largest, circular in shape, anterior pair eliptical, eye pigment brownish purple.

Pair of stout antennae, basally globular, widely separated, as long as palps. Pair of elongate palps, basally very swollen with long, triangular palpostyles. Longest tentacular cirri extending to setiger 3 (Fig. 8a).

Peristomium narrow ring, dorsally forming a narrow collar which overlaps base of prostomium, continues ventrally as narrow ring.

Pharynx not everted, dissected with pair of pale brown, sclerotised jaws with about 10 teeth. Elongate simple papillae, present on the oral ring only, arranged as follows: Area V=1, VI=1, VII–VIII=7.

Setiger 1 with elongate, narrow, triangular dorsal cirrus, and slightly shorter, triangular ventral cirrus. Neuropodium with small neuro-acicular papilla and large, triangular presetal ligule. Postsetal lobe broad and rounded, shorter than presetal ligule. Ventral neuropodial ligule triangular, slightly shorter than neuropodial presetal ligule.

From setiger 3, anterior setigers with broad-based dorsal cirrus, slightly shorter, triangular notopodial ligule with rounded postsetal lobe (Fig. 8b). Notopodial presetal ligule longer and notopodial postsetal lobe shorter than neuropodial ligules throughout. Neuropodia as described for setiger 1.

Parapodial lobes increase proportionally in size to approximately setiger 10, after which parapodial lobes gradually decrease in size and become less robust.

Ventral cirri bifid unequally from setiger 3, with ventralmost cirrus, initially approximately half length of primary cirrus, increasing in length posteriorly to become approximately three quarters its length by setiger 10 (Fig. 8c).

Dorsal cirri expanded, leaf-like and vascularised from setiger 11 (Fig. 8d), greatly exceed length of notopodial presetal ligule.

Setae include homogomph and sesquigomph spinigers and sesquigomph falcigers (Fig. 8e). Notosetae arranged in 2 bundles, 1 dorsal and 1 ventral to notopodial presetal ligule. Supra-acicular neurosetae arranged in U-shape around neuro-acicular papillae. Subacicular neurosetae dense, numerous, brush-like, occur posteriorly and ventrally to presetal neuropodial ligule. Holotype setal counts are shown in Table 8.

Dorsal transverse ridges occur on dorsum of setigers 10 to at least setiger 20, connecting parapodia together, at level of the dorsal cirri.

Pygidium unknown. Holotype not gravid.

**Variation.** Pigmentation varies from cream to pink in alcohol in the paratypes and the additional material examined. In all specimens the setae are straw-golden in colour, and very numerous on the first 10–15 setigers. All specimens have the following arrangement of pharyngeal papillae: Area V=1, VI=1, VII–VIII=5–7, with a distinct gap between VI and VIII. Ventral cirri are double from setiger

3–5 posteriorly, (most commonly from setiger 3). In small specimens it is difficult to detect the ventralmost branch. Dorsal transverse ridges occur in all specimens, and first appear at approximately setiger 10 and present on all subsequent setigers at least to setiger 36 (AHF POLY 1489).

**Remarks.** Banse (1977) revised the genus *Ceratocephale* Malmgren and recognised four species, *C. loveni* Malmgren, 1867; *C. pacifica* Hartman, 1960, *C. hartmanae* Banse, 1977 and *C. oculata* Banse, 1977. It is unclear as to Banse's (1977) opinion of *C. abyssorum* (Hartman & Fauchald, 1971) which Hartmann-Schröder (1977) transferred to *Ceratocephale*, although Banse does refer to her paper. At this stage, we accept this species as belonging to the genus.

In addition, a new species *C. andaman* has recently been

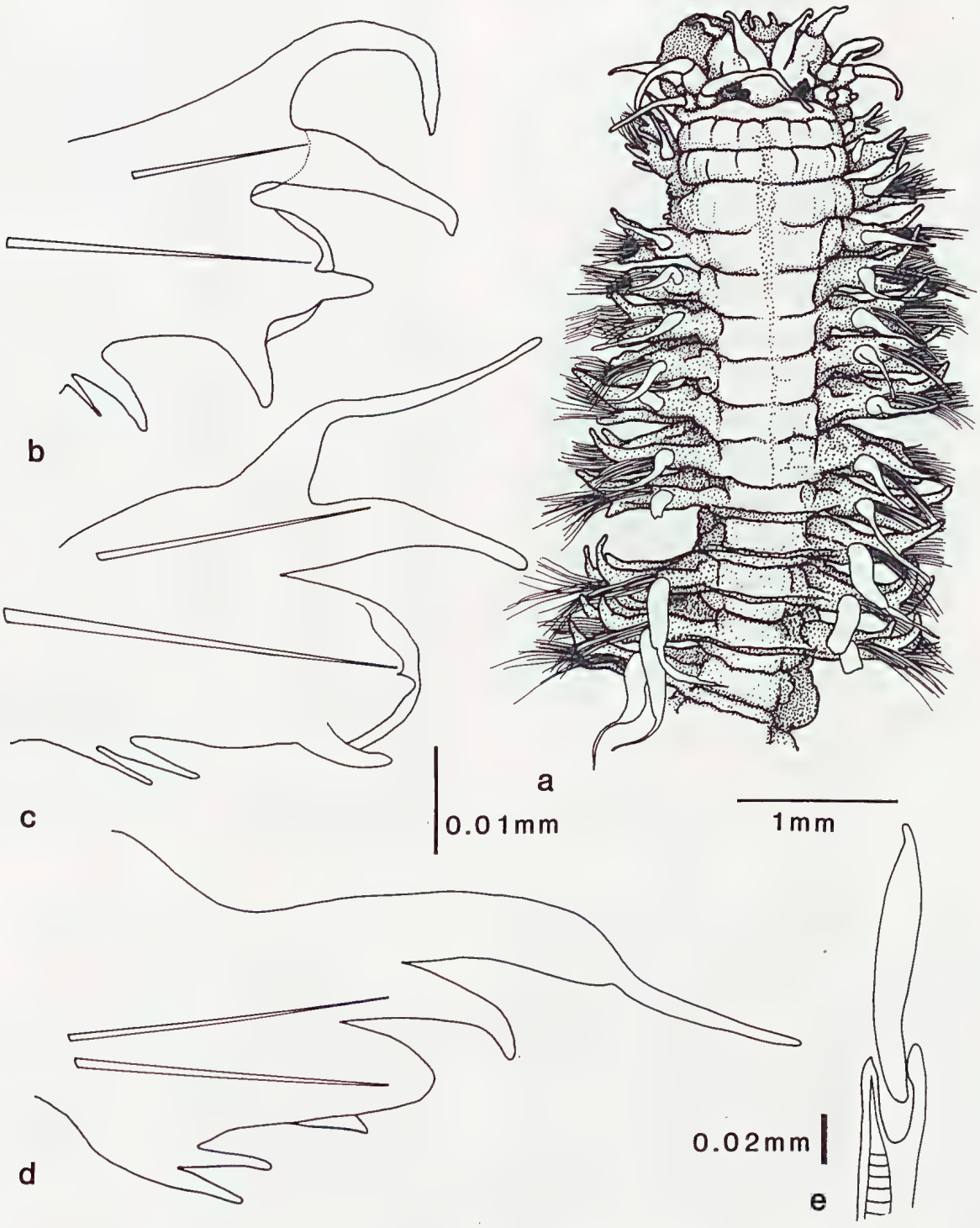


**Fig.8.** *Ceratocephale setosa* n.sp., holotype (AM W16093): a, anterior end, dorsal view; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 20; e, sesquigomph falciger, parapodium 3.

described by Hylleberg & Nateewathana (1988). In Table 9, the distinguishing characters of the currently recognised species of *Ceratocephale* are given. As can be seen from the Table, several of the previously described species are incompletely known, however a generic revision of the genus was beyond the scope of this study. As can be seen from the table, all *Ceratocephale* with the possible exception of *C. abyssorum* have mid-dorsal ridges, however the setiger at which ridges are visible is largely dependent upon the size and state of preservation of the specimen.

Although we have given information on the presence or absence of eyes, we believe this character should not be used as the sole character to distinguish species. *Ceratocephale oculata* Banse, and *Ceratocephale andaman* Hylleberg & Nateewathana have been described as with or without eyes suggesting that eye pigment is prone to fading, perhaps as a result of preservation in specimens of this genus.

Characters distinguishing *Ceratocephale setosa* n.sp. from other species of *Ceratocephale* are shown in Table 9.

**Habitat.** Occurs in muddy or silty sand in 15 to 55 m depth.

**Distribution.** Australia (Victoria, South Australia).

**Etymology.** The specific name is derived from the Latin *setosus* meaning bristly which refers to the numerous setae present on anterior parapodia.

### *Gymnonereis* Horst, emended

*Gymnorhynchus* Horst 1918: 247.—Pre-occupied by *Gymnorhynchus* Rudolphi, 1819; Cestoda (paper cited from Pettibone, 1970).

*Gymnonereis* Horst, 1919: 64.—Pettibone, 1970: 234.—Banse, 1977: 621–622 (in part).

**Type species.** *Gymnonereis sibogae* (Horst) 1918, by monotypy.

**Diagnosis.** Body elongate, depressed, attenuated posteriorly. Prostomium with frontal margin deeply incised between bases of frontal antennae.

Eversible pharynx with jaws having cutting edge smooth or serrated, with papillae on the oral ring. Notopodia with accessory dorsal cirri attached to dorsal cirrophores in anterior region only, with presetal ligules and short, rounded postsetal lobes. Median segments with dorsal cirrophores greatly elongated and highly vascularised (except in *G. crosslandi*) and lacking accessory cirri. Dorsal transverse ridges present or absent. Setae homogomph or sesquigomph spinigers and homogomph or sesquigomph falcigers may be present. Setae very numerous in anterior setigers.

**Remarks.** The above definition which is a synopsis of the generic diagnoses given by Pettibone (1970), Banse (1977) and Hylleberg & Nateewathana (1988), in part, has been modified to include species which have homogomph or sesquigomph falcigers. We have excluded reference to conspicuous presetal neuropodial ligules as this is not a character of *G. sibogae*.

*Gymnonereis* differs from another of the Gymnonereidinae *sensu* Fitzhugh, 1987, *Tambalagamia* which has vascularised dorsal transverse folds present, these folds are absent in *Gymnonereis*.

Pettibone (1970) synonymised *Tambalagamia* with *Gymnonereis* however Banse (1977) retained the genus due to the presence of these folds with the qualification that '...these skin folds are much more conspicuous than the narrow mid-dorsal flaps of *Ceratocephale hartmanae*'. Hylleberg & Nateewathana (1988) emended the generic diagnosis of *Gymnonereis* to include a new species (*G. phuketensis*) with large triangular mid-dorsal flaps thereby effectively synonymising *Tambalagamia* with *Gymnonereis*.

We have doubts about the validity of the genus *Tambalagamia* and suspect it should be synonomised with *Gymnonereis* but until the two genera have been thoroughly revised and type material re-examined we prefer to recognise them as separate genera.

The two new species from Australia, *G. yurieli* and *G. minyami* do possess dorsal ridges but they are not as well developed as those figured by Pillai (1961) or Banse (1977) for *Tambalamagia fauveli*. For this reason we have placed these two species in the genus *Gymnonereis* rather than *Tambalagamia*.

Banse (1977) recognises the following species of *Gymnonereis*, *G. sibogae* (Horst, 1918); *G. fauveli* (Hartmann-Schröder, 1962) and *G. crosslandi* (Monro, 1933).

The parapodia of *Gymnonereis* have been described partially following the terminology of Hylleberg & Nateewathana (1988). See also the remarks following the generic diagnosis of *Ceratocephale*. In cases where the dorsal cirri are paired or bifid, we have called the ventralmost branch of the pair the accessory dorsal cirrus. Hylleberg & Nateewathana (1988) call this branch the dorsal ligule.

### *Gymnonereis minyami* n.sp.

Fig. 9a–f, Tables 10, 12

**Material examined.** HOLOTYPE: Australia: South Australia, Upper Spencer Gulf 34°30'S, 136°55'E, 9.3 m, 26 Apr. 1979, 1(AM W202517), 13 mm long, 2 mm wide, 35 setigers. PARATYPES: Upper Spencer Gulf 34°30'S, 136°55'E, 7.3 m, 26 Apr. 1979, 1(AM W202518) 8.8 mm long, 1.9 mm wide, 27 setigers, 1(SAM E2129) 4 anterior fragments, 32°35'S, 137°46'E, 6 m, Nov. 1985, 1(AHF POLY 1487) 7.2 mm long, 0.9 mm wide, 30 setigers, 32°47.18'S, 137°50'E, 11 m, 1(BMNH ZB 1988.12) 9 mm long, 2.5 mm wide, 21 setigers, 33°05'S, 137°57.3'E, 6 m, Nov. 1985, 1(USNM 120511) 8 mm long, 2.5 mm wide, 21 setigers. All type material posteriorly incomplete. Non-type material: Upper Spencer Gulf, 32°42.2'S,

137°47.26'E, 15 m, (SAM E2122), 33°01'S, 137°38'E, 7 m, (SAM E2123), 32°35.04'S, 137°46.08'E, 6 m, (SAM E2124), 33°01'S, 137°37.38'E, 7 m, (SAM E2125), 33°01'S, 137°49'54'E, 12 m, (SAM E2126), 33°01'S, 137°49.54'E, 12 m, (SAM E2127), 32°40'S, 137°46.28'E, 13 m, (SAM E2128), incomplete all material collected Feb. 1986. Victoria: Bass Strait 40°14.4'S, 148°30.0'E, 60 m, 14 Nov. 1981 (NMV 5054); 39°03.2'S, 146°39.5'E, 55 m, 18 Nov. 1981 (NMV 5055). All non-type material posteriorly incomplete.

**Description.** Alcohol preserved animal, cream with golden setae, which are abundant on anterior setigers. Holotype not gravid.

Prostomium rectangular, deeply incised anteriorly

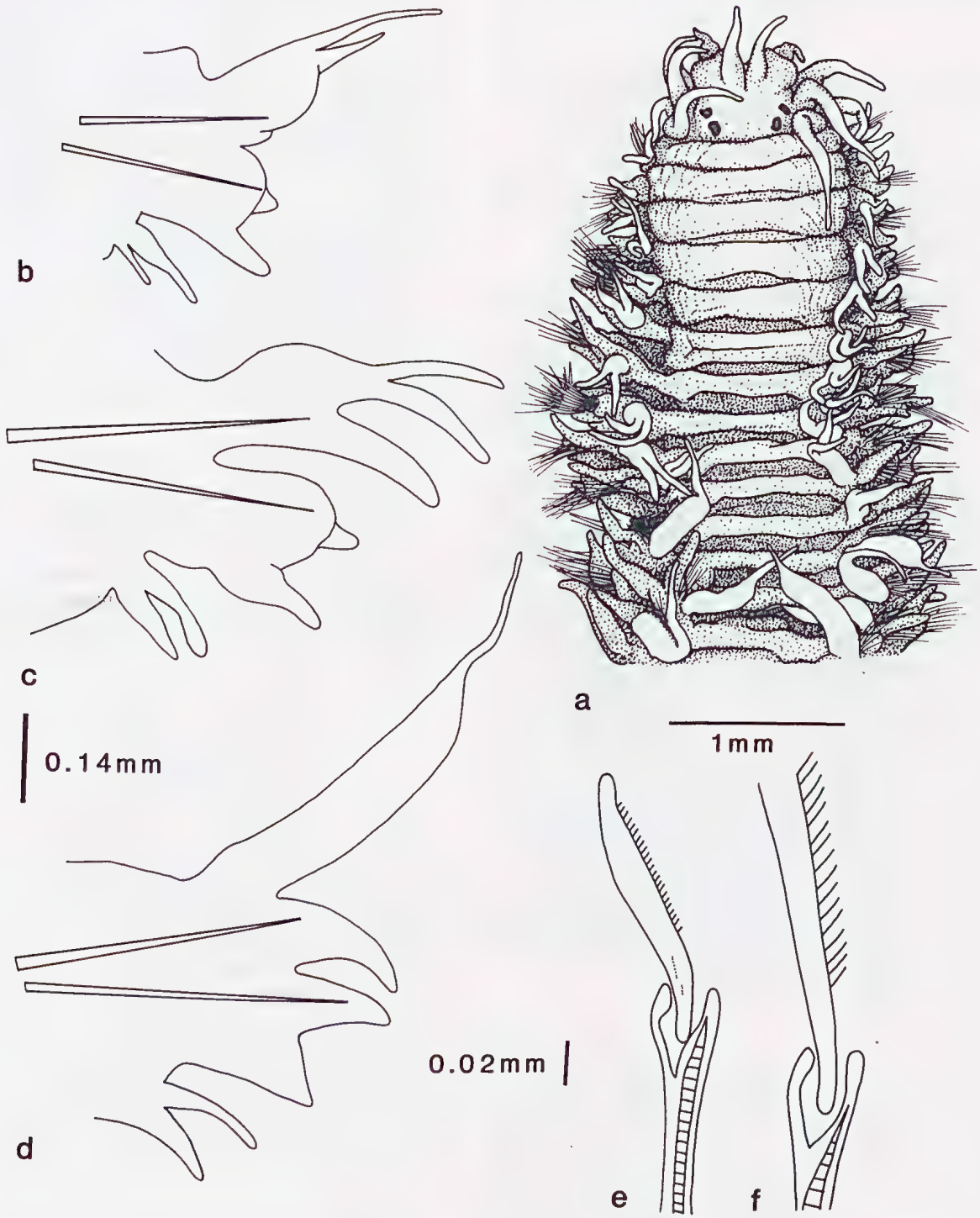


**Fig.9.** *Gymnonereis minyami* n.sp., holotype (AM W202517): a, anterior view, head end; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 20; e, sesquigomph falciger, parapodium 3; f, sesquigomph spiniger, parapodium 10 (part).

mid-dorsally, with a pair of stout antennae, longer than palps. Palps with swollen globular palpophores and short digitiform palpostyles. Eyes arranged basally and obliquely, anterior pair rectangular, posterior pair spherical (Fig. 9a). Longest tentacular cirri extending to anterior margin of setiger 3.

Peristomium narrow, pharynx with a pair of narrow jaws, heavily sclerotised along cutting margin, with 10–15 fine teeth. Papillae digitiform, present on oral ring arranged as follows: Area V=1, VI=1, VII–VIII=5, maxillary ring bare.

Setigers 1 and 2 with dark brown aciculum, tip curved and just emergent. Setigers 1–10 with bifid dorsal cirri. Accessory dorsal cirri anteriorly, two thirds length of dorsal cirri, posteriorly half as long as dorsal cirri. By setiger 11, dorsal cirrophore expanded, lamellate, appears vascularised, cirrostyle drawn out into fine tip. Lamellate dorsal cirri present on all subsequent setigers (35) on holotype.

Ventral cirrus unequally bifid on all setigers. Ventralmost branch one half-two thirds as long as primary branch.

Setiger 1, neuro-acicular papilla small, rounded and lies posteriorly to large triangular presetal ligule. Postsetal lobe rounded, shorter than presetal ligule. Ventral neuropodial ligule broad, subtriangular, slightly longer than inferior lobe.

Setiger 3 with basally swollen, triangular notopodial presetal ligule with a short, rounded postsetal lobe. Setae in 2 bundles, 1 either side of notopodial presetal ligule. Aciculum deeply embedded (Fig. 9b). Neuropodium as for setiger 1. Neurosetae in 2 fascicles with dorsalmost bundle arranged in a semicircle around neuro-acicular papilla and ventralmost bundle posterior and ventral to presetal ligule. This arrangement continues along length of animal. Remaining anterior parapodia as for setiger 3 (Fig. 9c,d).

Posteriorly, notopodial and neuropodial ligules and lobes decrease in size proportionately, with both notopodial and neuropodial postsetal lobes tending to triangular rather than ovoid shape.

Setae consist of homogomph and sesquigomph spinigers and sesquigomph falcigers present from setigers 2–7. Setal counts for the holotype are shown in Table 10.

Setigers 3–13, parapodia elongate and well separated from body wall, following parapodia compact and short. Transverse, dorsal raised-ridges connecting setigers 5–13, with ridges best developed on setigers 7–11.

Pygidium unknown.

**Variation.** The following variations are exhibited by the paratypes and additional material examined. The dorsal cirri are bifid from setiger 1 to setigers 9–11. Cirrophores are anteriorly expanded become narrower posteriorly after setigers 30–35. Ventralmost branch of ventral cirri is delicate and easily detached in small specimens. Transverse dorsal ridges occur from setiger 6–8. The exact number of following setigers on which transverse ridges occur is difficult to ascertain as all specimens are incomplete posteriorly, and the ridges become less prominent on posterior setigers. They are maximally developed on setigers 7–13.

Pharyngeal papillae are arranged as follows: Area V=1, VI=1, VII=5–7.

**Remarks.** Banse (1977), in a revision of *Gymnonereis* Horst, emended the generic diagnosis and recognised three species, *G. crosslandi* (Monro, 1933), *G. fauveli* (Hartmann-Schröder, 1962) and *G. sibogae* (Horst, 1918). *Gymnonereis minyami* n.sp. can be distinguished from *G. crosslandi* by the development of accessory dorsal cirri on the first 1 to 11 setigers, whereas in *G. crosslandi* they are restricted to the first 2 setigers. *Gymnonereis minyami* differs from *G. sibogae* in that the dorsal cirrus is expanded as a lamellate lobe from setiger 11, whereas in *G. sibogae* such an expansion does not occur until setiger 16. Toothed jaws are absent in the latter species and present in *G. minyami* n.sp. *Gymnonereis fauveli* completely lacks dorsal transverse ridges in contrast to *G. minyami* which has well developed dorsal ridges on setigers 5 to 13. These details are summarised in Table 12.

*Gymnonereis minyami* n.sp. closely resembles the other new species of *Gymnonereis, G. yurieli* n.sp. from Australia but can be distinguished by the presence of falcigers and fewer papillae on Areas VII–VIII in *G. minyami* n.sp. as shown in Table 12.

**Habitat.** Occurs in medium-coarse sand in 6 to 60 m.

**Distribution.** Australia (South Australia, Victoria)

**Etymology.** The specific name is derived from the Aboriginal word *minyama*, meaning many, referring to the large number of setae occurring in anterior setigers of this species.

### *Gymnonereis yurieli* n.sp.

Fig. 10a–d, Tables 11, 12

**Material examined.** HOLOTYPE: Australia: Queensland, Halifax Bay 19°10'S, 146°44'E, 5 m, Jan. 1977, (AM W202015), 9 mm long, 1 mm wide, 37 setigers, posteriorly incomplete. PARATYPES: Queensland, Halifax Bay 19°10'S, 146°38'E, 5 m, Jan. 1977, 1(AM W202622), 19°10'S, 146°38'E, 5 m, Jan. 1977 1(AM W202621), 4(NMV F54177), 19°09'S, 146°37'E, 5 m, Jan. 1977, 3(AHF POLY 1488), anterior fragments; 19°10'S, 146°38'E, 5 m, Jan. 1977, 1(BMNH ZB 1988.11), 7.5 mm long, 0.8 mm wide, 96 setigers, complete; 19°09'S, 146°37'E, 5 m, Jan. 1977, 4(USNM 120510), anterior fragments. All specimens with exception of BMNH ZB 1988.11 posteriorly incomplete. Non-type material: Moreton Bay, 1 specimen posteriorly incomplete (QM G10347).

**Description.** Alcohol preserved animal pale cream with dark brown acicula and numerous light golden setae on anterior setigers.

Prostomium with eyes arranged obliquely on lateral margins, posterior pair, slightly larger, both pairs dark

reddish brown. Prostomium squat, rectangular in shape with deep cleft between 2 antennae (Fig. 10a).

Palps with large, bulbous base and short, triangular palpostyle. Antennae as long as palps. Tentacular cirri with first pair longest extending to setiger 4, shortest extending to base of palps.

Peristomium narrow.

Pharynx with a pair of lightly sclerotised jaws with numerous teeth. Oral ring with papillae arranged as follows: Area V=1, VI=1, VII–VIII=8; maxillary row bare.

Setigers 1–11 with bifid dorsal cirri with accessory cirri slightly shorter than dorsal cirri. Ventral cirri bifid throughout. From setigers 11–22, dorsal cirrophores expanded and vascularised. On subsequent setigers, dorsal cirri narrow, elongate.

Setigers 1 and 2 with tip of aciculum slightly emergent.

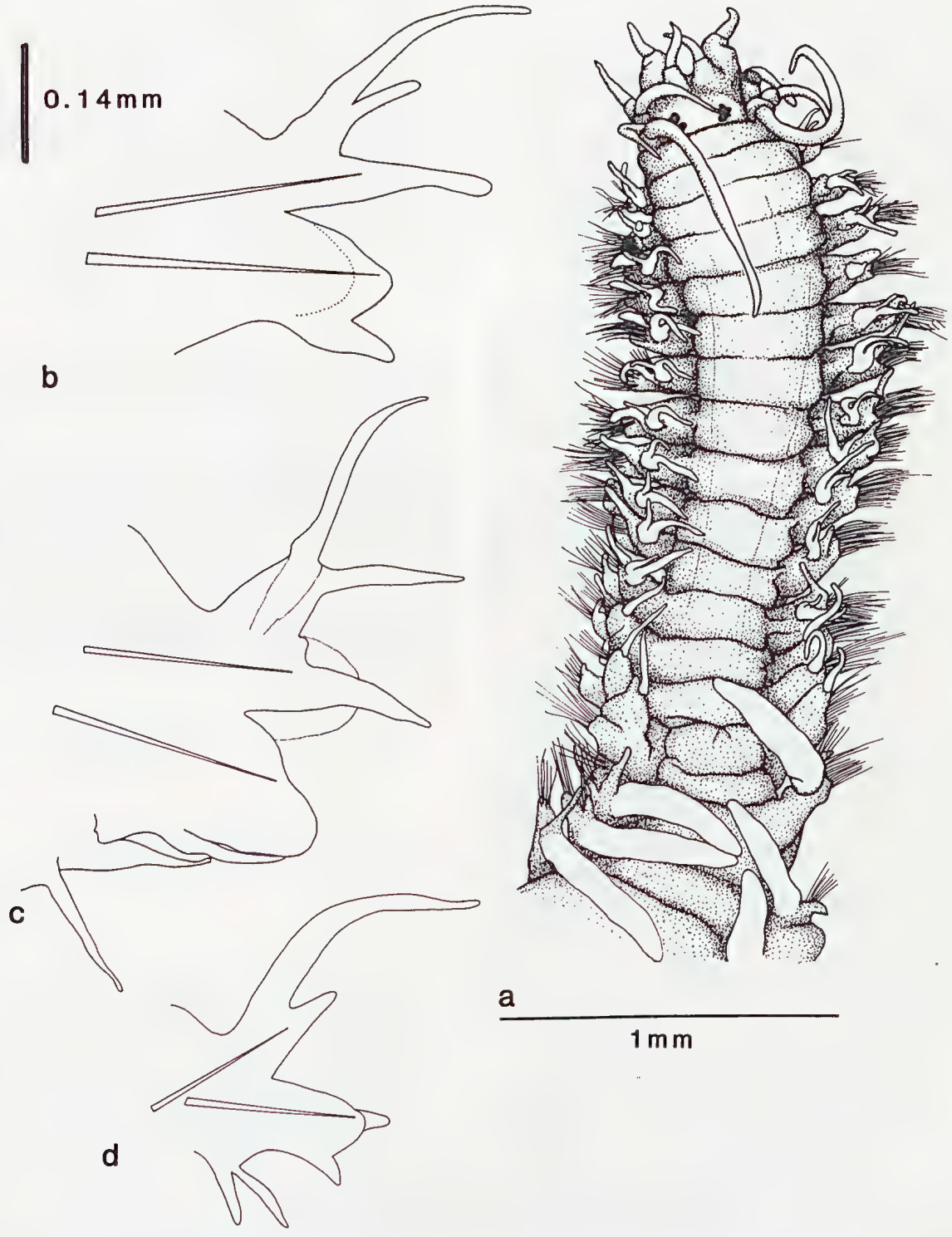


**Fig.10.** *Gymnonereis yurieli* n.sp., paratype (BMNH ZB 1988.11): a, anterior view, head end; b, anterior view of parapodium 3; c, anterior view of parapodium 10; d, anterior view of parapodium 50.

Setiger 1 with very small, rounded neuro-acicular papilla bearing the slightly emergent aciculum, large triangular presetal ligule and ventral ligule and rounded postsetal lobe. Presetal ligule equal in length to accessory dorsal ligule, exceeding length of postsetal lobe. Ventral ligule slightly shorter than presetal ligule. Setae arranged in 2 bundles, one dorsal to and other arranged in a semicircle around presetal ligule.

Setiger 3 (Fig. 10b), dorsal cirri and accessory dorsal cirri greatly elongate, exceeding length of all other parapodial lobes. Notopodia with broad based, triangular presetal ligule 1.5 times as long as neuropodial presetal ligule. Bluntly triangular postsetal lobe slightly exceeds neuropodial postsetal lobe in length.

Subsequent parapodia (Fig. 10c,d) as described for setiger 3, with lobes proportionately similar, but less robust and with fewer setae in posterior setigers. Ventral neuropodial ligule is reduced in size in far posterior setigers. Transverse dorsal ridges occur from setiger 10 as narrow raised-ridges connecting parapodia together, ridges continue to about setiger 19–20.

Notosetae consist of homo- and sesquigomph spinigers with laddered shafts and finely serrated blades. Neurosetae consist of sesquigomph spinigers with laddered shafts and blades either strongly or finely serrated. Neurosetae consist of short and long setae arranged in 2 fascicles. Setal counts for holotype are shown in Table 11.

These counts are approximate as the tufted arrangement of the setae often overlapping each other makes counting difficult, for this reason also, counts for homogomph and sesquigomph spinigers have been grouped as the difference between homogomph and sesquigomph shafts cannot be determined when setae are overlapping.

**Variation.** Only one paratype is complete (BMNH ZB 1988.11), has long anal cirri and last few segments are asetigerous and glandular. The type material, all from Halifax Bay, exhibits little variation.

The additional material (QM G10347) and (AM W15540) consist of incomplete animals which are considerably larger than any of the type material. However no differences can be detected between these larger specimens and the type material except in the number of setae, which are greater for both these specimens than the type material. This may be a function of size. The numerous, anterior setae are extremely robust and conspicuous, as are the dorsal transverse folds, in these larger specimens.

**Remarks.** *Gymnonereis yurieli* n. sp. differs from the three previously described species of *Gymnonereis*, *G. sibogai* Horst, 1918, *G. crosslandi* Monro, 1933 and *G. fauveli* Hartmann-Schröder, 1962, in having dorsal transverse ridges present from setiger 10. Such ridges are completely absent in these previously described species. The jaws of *G. yurieli* n.sp. are finely toothed whereas in *G. sibogai*, *G. crosslandi* and *G. fauveli* the jaws are smooth. *Gymnonereis yurieli* n.sp. lacks prominent mid-dorsal flaps which are present in *G. phuketensis* Hylleberg & Nateewathana, 1988.

*Gymnonereis yurieli* n.sp. can be separated from the other new species of *Gymnonereis minyami* n.sp. from Australia due to the presence of sesquigomph falcigers in *Gymnonereis minyami* n.sp. which are absent in *G. yurieli* n.sp. In Table 12 a summary of the diagnostic characters of the five species of *Gymnonereis* are given.

**Habitat.** Occurs on intertidal mud flats.

**Distribution.** Australia (Queensland).

**Etymology.** The specific name is derived from an Aboriginal word *yuriel* which means a coastal bay and refers to the type locality, Halifax Bay.

## *Olganereis* Hartmann-Schröder

*Olganereis* Hartman-Schröder, 1977: 147.

**Type species.** *Olganereis edmondsi* (Hartman, 1954), designated by Hartmann-Schröder, 1977.

**Diagnosis.** Prostomium subpyriform, with 2 pairs of eyes. Tentacular cirri with distinct cirrophores. First 2 setigers uniramous subsequent setigers biramous. In anterior notopodia, dorsal cirri at bases of dorsal notopodial ligule. Notopodia with 2 ligules and superior lobe. Neuropodia with conical or bilobed acicular lobes and ventral ligules. Ventral cirri tapered. Notosetae homogomph and heterogomph spinigers and heterogomph falcigers. Pharynx with papillae on both maxillary and oral rings.

### *Olganereis edmondsi* (Hartman)

*Ceratocephala edmondsi* Hartman, 1954: 23, figs 12–17.
*Olganereis edmondsi*.—Hartmann-Schröder, 1977: 147–149, pl. 2a–e, 3a–c.—Hutchings & Turvey, 1982: 138–139.

**Material examined.** Australia: Tasmania: Great Bay, Bruny Island 43°12'S, 147°22'E, 30 May 1974, 1(TASM K1106); Tamar Estuary, George Town 41°20'S, 147°02'E, Feb. 1984, 6(AM W198691). South Australia: Torrens Island 34°47'S, 138°32'E, 7 Mar. 1979 1(AM W18295); Kangaroo Island 35°50'S, 137°15'E, 8 Mar. 1978, 2(AM W18290), 7 Mar. 1978, many (AM W18291); 1 Mar. 1979, 1(AM W18292); 2 Mar. 1979, 3(AM W18293); 3 Mar. 1979, 1 (AM W18294); Port Augusta 32°30'S, 137°46'E, 14 Mar. 1979, 5(AM W18299); Coobowie, Yorke Peninsula 35°03'S, 137°43'E, 10 Feb. 1980, 2(AM W18460); Flinders Cairn, Port Lincoln 34°49'S, 135°47'E, 10 Mar. 1979, 6(AM W18296); Venus Bay, Inverloch 37°26'S, 140°51'E, 11 Mar. 1979, 1(AM

W18297), many (AM W18298), 27 Mar. 1981, many (AM W18597). Western Australia: Albany 35°03'S, 117°53'E, 14 Jan. 1988, 1(AM W202836).

All specimens collected intertidally.

**Description.** Pharynx with long, fine papillae arranged as follows: Area I = 0–1, II = 0, III–IV = 3-6, V = 0, VI = 1, VII–VIII = 7–12. Anterior notopodia, dorsal cirri exceed length of dorsal and median ligules. Notopodial lobes subtriangular, superior lobe present. Neuropodia with bilobed acicular lobe and postsetal lobe of equal length. Ventral ligule conical. Posteriorly, dorsal cirri greatly exceed length of remaining lobes. Dorsal ligule and superior lobe greatly reduced. Acicular lobes not distinctly bilobed. Postsetal lobe exceeds acicular lobe in length. Ventral ligule reduced. Ventral cirrus exceeds length of ventral ligule throughout. Notosetae homogomph spinigers. Supra-acicular neuropodia with homogomph spinigers and 1–4 robust, heavily sclerotised heterogomph falcigers. Subacicular neuropodia with heterogomph spinigers and falcigers.

**Remarks.** This genus is monospecific, and occurs only in southern Australia. Material varies from the original description and from paratype redescribed by Hartmann-Schröder (1977) only in the number of papillae. Hartmann-Schröder (1977) gives number of papillae in Area I = 1, III–IV = 5 and VII–VIII = 9. These differences can be attributed to variation in size and distributional range of material examined in this study and does not warrant specific distinction.

**Habitat.** Occurs on intertidal sand and mud flats, often associated with mussel clumps, *Zostera* seagrass beds and encrusting fauna, in fibrous tubes embedded with sand grains.

**Distribution.** Australia (Victoria, Tasmania, South Australia, Western Australia).

## *Websterinereis* Pettibone

*Websterinereis* Pettibone, 1971: 19–20.

**Type species.** *Nereis tridentata* Webster, 1880, designated by Pettibone, 1971.

**Diagnosis.** Prostomium with 2 pairs of eyes. Pharynx with papillae on oral ring, large papillae on Area VI and single row of minute papillae on Areas VII–VIII.

Notopodia with 2 ligules and usually superior lobe present. Neuropodia with postsetal lobes and ventral ligules, with or without presetal lobes distinct from acicular lobes. Ventral cirri short, tapered. Notosetae homogomph spinigers only. Neurosetae homogomph and heterogomph spinigers and heterogomph falcigers.

### *Websterinereis foli* (Fauvel)

*Leptonereis foli* Fauvel, 1930: 520–522, fig. 3.
*Laeonereis foli*.—Hartman, 1948: 55–56, 1959: 245.
*Ceratocephala* (sic) *corallicola* Reish, 1968: 215–217, fig. 4 (1–5).
*Websterinereis foli*.—Pettibone, 1971: 23–25, figs 10a–h, 11a–k.

**Material examined.** Australia: Western Australia: Port Murat, Exmouth Gulf 21°51'S, 114°10'E, 27 Apr. 1972, 1(AM W202516); New South Wales: Long Reef 33°45'S, 151°19'E, 41 m, 27 Apr. 1972, 1(AM W6879). South Australia: Spencer Gulf, Eastern Shoal 33°05'S, 137°49.8'E, Feb. 1986, 8 m, 1(SAM E2351), 33°01'S, 137°45'E, Feb. 1986, 15 m, 1(SAM E2352), Mangrove Point 33°02.24'S, 137°37.88'E, no date, 10 m, 1(SAM E2354); Whyalla, 32°42.20'S, 137°47.26'E, Aug. 1986, 15 m, 1(SAM E2353).

**Description.** Material examined ranges in size from 11–30 mm long (complete specimens), 0.3–0.6 mm wide and up to 131 setigers. Prostomium with mid-dorsal depression. Peristomium uniformly rust coloured, anterior setigers with narrow bands of pigment. Pharynx, maxillary ring without paragnaths or papillae, oral ring with single large papillae on Area VI and a row of 6–7 smaller papillae on Areas VII–VIII.

Anterior parapodia with triangular dorsal and median ligules and shorter but prominent superior lobe. Dorsal cirri long, tapering, exceed length of dorsal ligules. Neuropodia with shorter, triangular acicular and postsetal lobes. Ventral ligule conical, ventral cirrus triangular, tapering. Posterior parapodia as for anterior parapodia with dorsal ligule increasing gradually in size. Ventral ligule slightly exceeds length of acicular lobe.

Notosetae homogomph spinigers. Supra-acicular neurosetae with homogomph spinigers and short heterogomph falcigers. Falcigers robust with short blades and broad shaft with distal thickening of boss at the point of blade insertion. Subacicular neurosetae with heterogomph falcigers. These falcigers blades relatively longer in anterior than posterior parapodia. Posterior parapodia sometimes with single short-bladed heterogomph spiniger in subacicular bundle of neurosetae.

**Remarks.** Agrees well with Pettibone's (1971) description. Specimens are small, and pharyngeal papillae difficult to detect and could be overlooked. Pigmentation varies, some specimens more heavily pigmented anteriorly than others.

This is the first record of the species from Australia and represents a considerable range extension.

**Habitat.** The Australian material was collected from depths of 10 to 41 m, and in Spencer Gulf in coarse sand. Non-Australian material collected has been associated with coral habitats.

**Distribution.** Australia (Western Australia, New South Wales, South Australia), Central Pacific (New Caledonia, Marshall Islands).

### *Websterinereis punctata* (Wesenberg-Lund)

*Leptonereis punctata* Wesenberg-Lund, 1949: 289, figs 21–23.
*Laeonereis anklyoseta* Day, 1957: 83–84, fig. 5a–j; 1960: 321.—Hartman, 1959: 243.
*Nicon punctata*.—Hartman, 1958: 265–266; 1959: 245, 274.
*Websterinereis punctata*.—Pettibone, 1971: 25–27, fig. 12a–i, fig. 13a–h.—Stephenson *et al.*, 1974: 112.

**Material examined.** Australia: Queensland: Moreton Bay, Peel Island 27°30'S, 153°21'E, 1(QM G10477); Bramble Bay 27°18'S, 153°06'E, 1(QM GH4039).

**Description.** Material examined 1.9–3.5 mm wide, posteriorly incomplete, maximum length 70 mm with 78 setigers. Maxillary ring of pharynx bare, without paragnaths or papillae. Oral ring with single large papillae on Area VI and a row of 6–7 small papillae on Areas VII–VIII.

Anterior parapodia, notopodia with long triangular dorsal and median ligules. Dorsal ligule exceeds length of median ligule. Superior lobe present, slightly shorter than median ligule. Dorsal cirrus conical slightly shorter than dorsal ligule. Neuropodia with bluntly rounded acicular lobe and longer triangular postsetal lobe. Ventral ligule triangular, approximately equal to postsetal lobe in length. Posterior parapodia, dorsal cirri exceed length of dorsal ligule. Superior lobe reduced. Remaining as for anterior parapodia. Notopodial and neuropodial lobes widely spaced posteriorly. Notosetae long bladed homogomph spinigers. Anterior parapodia supra-acicular neurosetae with homogomph spinigers and long bladed heterogomph falcigers. Subacicular neuropodia with long bladed heterogomph spinigers dorsally, long bladed heterogomph falcigers and short bladed heterogomph spinigers ventrally.

Median and posterior parapodia, supra-acicular neurosetae, long bladed heterogomph falcigers replaced by stout heterogomph falcigers with bifid tips. Medially, blades partially fused to shaft and posteriorly blades and shafts completely fused. Subacicular neuropodial falcigers and spinigers short bladed medially. Posteriorly, subacicular neuropodial falcigers as for anterior parapodia.

**Remarks.** Agrees well with Pettibone's (1971) description. This species is also very similar in features of the parapodia and setae to *Nicon japonicus* Imajima, 1972, however *Websterinereis punctata* can be distinguished due to the presence of papillae on the oral ring, which are absent in *N. japonicus*.

**Habitat.** In Australia the species occurs in sandy mud and shelly sand in Moreton Bay in depths of 4 m. This species has been collected in 49 to 59 m in the Persian Gulf and 2 to 55 m in South Africa. Habitat includes sand, clay, mud, shells and coral.

**Distribution.** Australia (Queensland), Persian Gulf (northern and central part), South Africa, Natal, Mozambique.

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## Appendix

Table 1. The variation in the distribution and type of setae along the body of Australian material (10 individuals) of *Nicon moniloceras*. (see Introduction for abbreviations).

| Parapodia | | | homogomph spinigers | heterogomph spinigers | heterogomph falcigers |
|---|---|---|---|---|---|
| 3 | noto | | 4–7 | 0 | 0 |
| | neuro | supra | 3–7 | 0 | 1–4 |
| | | sub | 0 | 6–10 | 0 |
| 10 | noto | | 7–15 | 0 | 0 |
| | neuro | supra | 5–8 | 0 | 2–4 |
| | | sub | 0 | 6–11 | 1–2 |
| 20 | noto | | 7–15 | 0 | 0 |
| | neuro | supra | 4–7 | 0 | 2–4 |
| | | sub | 0 | 6–11 | 2–6 |
| 50 | noto | | 7–8 | 0 | 0 |
| | neuro | supra | 3–4 | 0 | 2–3 |
| | | sub | 0 | 2–3 | 3–4 |

Table 2. Distribution and type of setae along the body of *Nicon rotunda* n.sp. holotype (holo) and six paratypes (para). Counts for paratypes are shown in brackets.

| Parapodia | | | homogomph spinigers | | homogomph falcigers | | heterogomph falcigers | |
|---|---|---|---|---|---|---|---|---|
| | | | holo | para | holo | para | holo | para |
| 3 | noto | | 15 | (2–8) | 0 | | 0 | |
| | neuro | supra | 8 | (2–4) | 0 | | 0 | (2–3) |
| | | sub | 3 | (0–4) | 10 | (2–6) | 11 | (2–7) |
| 10 | noto | | 18 | (1–14) | 0 | | 0 | |
| | neuro | supra | 8 | (3–7) | 0 | | 3 | (1–4) |
| | | sub | 3 | (0–3) | 6 | (2–7) | 12 | (3–7) |
| 20 | noto | | 1 | (3–12) | 0 | | 0 | |
| | neuro | supra | 13 | (2–6) | 0 | | 3 | (2–4) |
| | | sub | 3 | (0–3) | 2 | (1–9) | 9 | (3–6) |
| 50 | noto | | 15 | (3–7) | 0 | | 0 | |
| | neuro | supra | 8 | (2–4) | 0 | | 2 | (1–2) |
| | | sub | 7 | (2–4) | 0 | | 4 | (2–4) |

Table 3. The diagnostic features of the species of *Nicon*. *See comments *Websterinereis punctata* page. **Poorly known species - Pettibone (1971) suggests probably not *Nicon*. Supra – neuropodial supra-acicular setae, sub – subacicular setae. Question marks indicate shaft type eg. homogomph or hetergomph not known. Neuropodial position (i.e. supra or subacicular) not known for *N. abyssalis*, *N. polaris* and *N. yaguinae*. Abbreviations: ho sp = homogomph spinigers, he sp = heterogomph spinigers, ho f = homogomph falcigers, he f = heterogomph falcigers.

| Species | Setae (Neuropodia) | ho sp | he sp | ho f | he f | Diagnostic features | Distribution |
|---|---|---|---|---|---|---|---|
| *Nicon maculata* Kinberg, 1866 | supra- | x | | | x | Neuropodia conical acicular lobe, digitiform postsetal lobes. Anterior neuropodial ligules, thick, rounded. Neuropodial (supra) falcigers thickened posteriorly. | Antarctic and subantarctic waters, East and South China Seas, southern Australia. |
| | sub- | x | | | x | | |
| *Nicon moniloceras* Hartman, 1940 | supra- | x | | | x | Notopodial ligules digitiform, subequal. Rudimentary superior lobe. Dorsal notopodial ligule reduced posteriorly. Median neuropodial falcigers recurved distal tooth with distinct tendon. Long tentacular cirri. | Eastern Australia, California – western Mexico Japan. |
| | sub- | | x | | x | | |
| *Nicon aestuarensis* Knox, 1951 | supra- | x | x | | x | Notopodial ligules conical, superior lobe short. Neuropodia bilobed acicular lobe, conical postsetal lobes. | New Zealand. |
| | sub- | | x | | x | | |
| *Nicon abyssalis*** Hartman, 1967 | | x? | x | x? | x? | Eyes absent. Peristomium long; dorsal notopodial ligule reduced, median ligule elongate posteriorly. Falcigers with elongate blades. | South Shetland Islands, Antarctic Peninsula. |
| *Nicon polaris*** Hartman, 1967 | | x? | x? | x? | x? | Prostomium posterior margin with prolonged lappets. | Bransfield Strait, Antarctica. |
| *Nicon japonicus** Imajima, 1972 | supra- | x | | | x | Ventral ligules reduced posteriorly. Distally recurved falcigers. Median parapodia with 2 pseudocompound neurosetae (supra) with bifid tips. Simple setae posteriorly. | Southern Japan. |
| | sub- | | x | | x | | |
| *Nicon yaguinae* Fauchald, 1977 | | x | x | | x | Anteriorly, acicular lobes longer than postsetal lobes; posteriorly, postsetal longer. Neuropodial acicular lobe truncate. | Oregon, U.S.A. |
| *Nicon sinica* Wu & Sun, 1979 | supra- | x | | | x | Notopodial ligules conical. Neuropodial acicular lobe rounded, postsetal lobe digitiform. Median posterior falcigers short bladed with recurved tips. | Yellow and South China Sea |
| | sub- | | x | | x | | |
| *Nicon rotunda* n.sp. | supra- | x | | | x | Notopodial ligules conical anteriorly, triangular posteriorly. Neuropodia, acicular and postsetal lobes equal length. Anterior neuropodial ligules thick, rounded. Homogomph falcigers in neuropodia (sub) of anterior setigers. | Northern and eastern Australia |
| | sub- | x | | x | x | | |

Table 4. The variation in the distribution and type of setae along the body of Australian material (20) of *Dendronereides heteropoda*.

| Parapodia | | | homogomph and sesquigomph spinigers | homogomph falcigers |
|---|---|---|---|---|
| 3 | noto | | 4–11 | 0 |
| | neuro | supra | 7–24 | 2–8 |
| | | sub | 11–24 | 3–7 |
| 10 | noto | | 8–21 | 0 |
| | neuro | supra | 7–21 | 4–7 |
| | | sub | 11–24 | 4–12 |
| 20 | noto | | 7–25 | 0 |
| | neuro | supra | 5–23 | 3–6 |
| | | sub | 5–30 | 3–7 |
| 50 | noto | | 4–10 | 0 |
| | neuro | supra | 12–20 | 2–4 |
| | | sub | 0 | 0 |

Table 5. The variation in the distribution and type of setae along the body of Australian material (14) of *Dendronereides zululandica*.

| Parapodia | | | homogomph spinigers | heterogomph spinigers | homogomph falcigers | heterogomph falcigers |
|---|---|---|---|---|---|---|
| 3 | noto | | 3–7 | 0 | 0 | 0 |
| | neuro | supra | 3–7 | 4–6 | 0 | 3–5 |
| | | sub | 0 | 5–11 | 0 | 4–9 |
| 10 | noto | | 2–9 | 0 | 0 | 0 |
| | neuro | supra | 2–6 | 3–4 | 3–6 | 3–6 |
| | | sub | 0 | 3–7 | 0 | 2–6 |
| 20 | noto | | 3–4 | 0 | 0 | 0 |
| | neuro | supra | 3–5 | 0 | 0 | 0 |
| | | sub | 0 | 4–6 | 2–6 | 2–6 |
| 50 | noto | | 2–3 | 0 | 0 | 0 |
| | neuro | supra | 6–9 | 2–6 | 1–3 | 0 |
| | | sub | | | | |

Table 6. Distribution and type of setae along the body of the holotype (AM W202515) of *Ceratocephale aureola* n.sp.

| Parapodia | | | homogomph spinigers | sesquigomph spinigers | sesquigomph falcigers |
|---|---|---|---|---|---|
| 3 | noto | | 2 | 3 | 0 |
| | neuro | supra | 0 | 12* | 2 |
| | | sub | 0 | 15** | 2 |
| 10 | noto | | 0 | 14 | 0 |
| | neuro | supra | 0 | 18 | 0 |
| | | sub | 0 | 21 | 0 |
| 20 | noto | | 0 | 18 | 0 |
| | neuro | supra | 0 | 15 | 0 |
| | | sub | 0 | 20 | 0 |
| 50 | noto | | 0 | 11 | 0 |
| | neuro | supra | 12 | 0 | 0 |
| | | sub | 12 | 0 | 0 |

Notes:
* 4 short bladed, 7 long bladed, 1 with broad blade with long teeth or serrations
** 9 long bladed, 5 short bladed, 1 with broad blade with long teeth or serrations
Anteriorly spinigers primarily sesquigomph, posteriorly tending to homogomph. From setiger 10, all spinigers are long bladed.

Table 7. The variation in the distribution and type of setae along the body of Australian material (2) of *Ceratocephale ?pacifica.*

| Parapodia | | | homogomph spinigers | sesquigomph spinigers |
|---|---|---|---|---|
| 3 | noto | | 9 | 0 |
| | neuro | supra | 2 | 6 |
| | | sub | 3 | 3 |
| 10 | noto | | 4–10 | 9 |
| | neuro | supra | 0 | 8–10 |
| | | sub | 1–10 | 0–5 |
| 20 | noto | | 4 | 18 |
| | neuro | supra | 0 | 18 |
| | | sub | 0 | 15 |

Table 8. Distribution and type of setae along the body of holotype (AM W16093) of *Ceratocephale setosa* n.sp.

| Parapodia | | | homogomph spinigers | sesquigomph spinigers | sesquigomph falcigers |
|---|---|---|---|---|---|
| 3 | noto | | 0 | 6 | 0 |
| | neuro | supra | 0 | 14 | 0 |
| | | sub | 0 | 13 | 7 |
| 10 | noto | | 8 | 0 | 0 |
| | neuro | supra | 0 | 18 | 8 |
| | | sub | 0 | 21 | 0 |
| 20 | noto | | 5 | 0 | 0 |
| | neuro | supra | 0 | 10 | 0 |
| | | sub | 0 | 17 | 0 |

Table 9. The diagnostic features of the species of *Ceratocephale*. *Eyes originally recorded, but no longer visible on type. # Ridge mid-dorsally a high, narrow flap. ** Ventral setae described as slightly falcigerous.

| Species | Eye spots | First bifid ventral cirri (parapodia) | Setigers with expanded dorsal cirrophores | Setigers with dorsal cirrophores connected by low ridges | Setae | Papillae (oral ring) |
|---|---|---|---|---|---|---|
| *Ceratocephale loveni* Malmgren, 1867 | absent* | 3 | 10 onwards | ? 6 onwards | ho sp, ses sp | Dorsally 3 Ventrally 2 rows : 7 and 3. |
| *Ceratocephale pacifica* Hartman, 1960 | absent | 1 | 8 onwards | 8 onwards | ho ses | Unknown. |
| *Ceratocephale abyssorum* Hartman & Fauchald, 1971 | absent | 1 | ?all | ? absent | ho sp** | Unknown. |
| *Ceratocephale hartmanae* Banse, 1977 | absent | 3 | ? unknown | 9 onwards # | ho sp | I row, 3 dorsal 7 ventral. |
| *Ceratocephale oculata* Banse, 1977 | present | 1 | 10 onwards | 4 onwards | ho sp | Unknown. |
| *Ceratocephale andaman* Hylleberg & Nateewathana, 1988 | present or absent | 1 | 8 or 9–30 | 5–12 sometimes # | ho sp | V–VI=3, VII–VIII=7 |
| *Ceratocephale aureola* n.sp. | present | 1 | 10 onwards | 10 onwards | ho sp, ses sp, ses f | V=1, VI=1, VII–VIII=7 |
| *Ceratocephale setosa* n.sp. | present | 3 | 11 onwards | absent | ho sp. ses sp ses f | V=1, VI=1, VII–VIII=5–7. |

Table 10. Distribution and type of setae along the body of holotype (AM W202517) of *Gymnonereis minyami* n.sp.

| Parapodia | | | homogomph spinigers | sesquigomph spinigers | sesquigomph falcigers |
|---|---|---|---|---|---|
| 3 | noto | | 0 | 9 | 0 |
| | neuro | supra | 14 | 0 | 1 |
| | | sub | 0 | 17 | 6 |
| 10 | noto | | 9 | 4 | 0 |
| | neuro | supra | 9 | 0 | 0 |
| | | sub | 0 | >18 | 0 |
| 20 | noto | | 15 | 0 | 0 |
| | neuro | supra | 12 | 0 | 0 |
| | | sub | 15 | 0 | 0 |

Table 11. Distribution of setae along the body of holotype (AM W202015) of *Gymnonereis yurieli* n.sp.

| Parapodia | | | homogomph and sesquigomph spinigers |
|---|---|---|---|
| 3 | noto | | 18 |
| | neuro | supra | 11 |
| | | sub | 22 |
| 10 | noto | | 20 |
| | neuro | supra | 20 |
| | | sub | 26 |
| 20 | noto | | 17 |
| | neuro | supra | 11 |
| | | sub | 14 |

Table 12. The diagnostic features of the species of *Gymnonereis*.

| Species | Jaw teeth | Oral ring papillae (Area) | Setigers with dorsal cirri bifid | Setae | Setigers with dorsal transverse 1. ridges 2. prominent flaps | Setigers with enlargement of dorsal cirrophores |
|---|---|---|---|---|---|---|
| *Gymnonereis sibogae* Horst, 1918 | absent | V–VI=3<br>VII–VIII=7 | 1–10 | ho sp<br>ses sp<br>*ses f | absent | 15 or 16 ? |
| *Gymnonereis crosslandi* Monro, 1933 | absent | V=1, VI=1,<br>VII–VIII=7<br>+ 3 pairs short transverse ridges | Setigers 1 and 2 only | sp | absent | absent |
| *Gymnonereis fauveli* Hartmann-Schröder 1962 | absent | V–VI=5<br>VII–VII=7 | 3–14 | ho sp<br>ses sp | absent | 15–50 or 60 |
| *Gymnonereis phuketensis* Hylleberg & Nateewathana, 1988 | present or absent | V=VI=3<br>VII=VIII=7 | 1–13 | ho sp<br>**ses sp | 2. present on setigers with enlarged cirrophores | 14 for 10–24 setigers |
| *Gymnonereis minyami* n.sp | present | V=1, VI=1<br>VII=VIII=5–7 | 1–11 | ho sp<br>ses sp<br>se f | 1. present setigers 5–13 | 11–30 or 35 |
| *Gymnonereis yurieli* n.sp. | present | V=1, VI=1<br>VII=VIII=8 | 1–11 | ho sp<br>ses sp | 1. present from setigers 10–20 | 11 onwards |

N.B. Ventral cirri are bifid on all setigers in each species. *These were described by Pettibone (1970) as spinigers with short blunt blades. ** Described by Hylleberg & Nateewathana (1988) as slightly heterogomph.

# A Re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a Discussion of the Genus

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ABSTRACT. Like so many other serpulid genera, *Ditrupa* has a history of taxonomic confusion, even to the extent that the worm tubes have been included in the Mollusca by some workers. In recent publications, most authors follow Fauvel (e.g. 1953) and recognise a single species, *Ditrupa arietina* O.F. Müller, 1776, worldwide, despite the fact that descriptions of this species were based on European and Atlantic material. A re-examination of type specimens and study of a broad range of samples from the Indo-Pacific now justifies the recognition of a separate species, *Ditrupa gracillima* Grube, 1878, from this region. It shows extreme variation, at least partly related to depth: from 100 m downwards an ecophenotype prevails, previously described as *D. arietina* var. *monilifera*.

HOVE, H.A. TEN & R.S. SMITH, 1990. A re-description of *Ditrupa gracillima* Grube, 1878 (Polychaeta, Serpulidae) from the Indo-Pacific, with a discussion of the genus. Records of the Australian Museum 42 (1): 101–118.

*Ditrupa* Berkeley, 1835 is a genus of serpulid polychaete found living unattached in soft sediment marine environments around the world. The worms are clearly recognisable from other serpulids by their anatomy, behaviour and distinctive tusk-shaped tubes. Despite this, most descriptions are poor, having been based solely on dredged calcareous tubes, most often devoid of the polychaete. The worms and their tubes can form a significant component of the muddy benthic community. In the Atlantic, *Ditrupa* is sometimes found in populations of over 1000/m$^2$ (Dyer *et al.*, 1982:310) and may account for more than 50% of the biogenic carbonate sediments (Wilson, 1979:M87). Fossil *Ditrupa* may be so abundant that they are used as key beds for geological field work, and to deduce the direction of prevalent palaeocurrents (Cheng, 1974). Although a number of Recent species has been erected in the past, most authors currently follow Fauvel (e.g. 1953:470), who recognises only a single species, *Ditrupa arietina*, worldwide.

There has always been considerable confusion in the classification of *Ditrupa* (sometimes spelled *Ditrypa*). In the 18th and 19th centuries particularly, as well as more recently, species were misidentified as the scaphopod genus *Dentalium* Linnaeus, 1758 and vice versa. For

example, *Dentalium perpusillus* Sowerby, 1832 had been placed in *Ditrupa* by Mörch (1863:427), but is correctly referred to *Cadulus* (*Gadila*) *perpusilla* by Emerson (1971:77; material studied BMNH 1950.10.10.1-5). Moreover, *Dentalium*'s have frequently been mistaken for *Ditrupa*, for example by Fauvel & Rullier (1959:196). In view of this, in future all possible synonyms given below should be checked against the material, if it is still in existence. As another example, Fauvel's 1932 record from a depth of 1,500 m is suspect as it exceeds the known depth limit for living specimens (650 m, reported herein) by 850 m.

No wonder that in fossil literature the confusion is worse. Even authors who tried to base fossil upon Recent taxonomy by using Recent material for comparative purposes, sometimes misinterpreted the genus *Ditrupa* completely. Lommerzheim (1979:143–145, pl.15 figs 1–4) attributes three species with a fixed, generally triangular apical tube-part to *Ditrupa*, while Recent representatives are free-living and even the youngest tube-parts are always circular in diameter, without a trace of an adnascent part. In our opinion it is unlikely that the many fossil species with angular tubes attributed to *Ditrupa* really belong to this genus — for instance, *D. canteriata* (Hagenow, 1840), *D. retusa* and other species by Regenhardt (1961) and *D. tricostata* (Goldfuss, 1841). "*Ditrupa*" *mosae* (Bronn, 1837) already has been referred to the genus *Sclerostyla* by Cupedo (1980).

In this paper, attention is focused on *Ditrupa* from the Indo-Pacific region. Though commonly found, *Ditrupa* is not well known from these waters. Examination of Recent northern Australian specimens with variable tube appearance suggested to us the possibility of one or more species co-existing in the area. Certainly, the worms did not appear to fit within *D. arietina* of the Atlantic, of which a diagnosis is given for comparative purposes. The examination of type material of *Dentalium laevis* Brazier, 1877 in the collections of the Australian Museum and of *Ditrypa gracillima* Grube, 1878 in the Museums of Wroclaw and Berlin, coupled with the availability of a large amount of new and much unworked material, has made a partial revision of this confusing genus possible.

## Materials and Methods

Material studied existed in several forms. Empty tubes were examined from either dry or wet collections. Where entire animals were preserved in wet collections, it was found that specimens could be pushed from their tubes by inserting a horse hair gently into the apex (i.e. the narrow posterior end). In this way, breaking the tube into fragments could be avoided. The live material examined was maintained for several weeks in a closed aquarium system.

Ten Hove & Jansen-Jacobs (1984) proposed a standard method which seeks to avoid data from juveniles influencing the descriptions of the adult worms. Essentially their method is used in this paper.

The following parameters were noted for each worm: length and width of animal, length of radioles, termination of thoracic membranes, number of both thoracic and abdominal setigers, number of radioles on left and right side of body, point of insertion of peduncle, length and width of operculum, and the shape of setae in first setiger. The mean and standard deviations have been computed from non-juvenile specimens with a thoracic width of at least 50% of the maximum observed width. For example, the notation (30)32–**36.8**–40 (SD=2.3, n=10) means that the number of abdominal segments observed is 30–40, but that SD and mean (36.8) have been computed over ten non-juvenile specimens in which the range was 32–40.

An attempt was made to discern populations from their tubes. For this purpose eight measurements were taken in the large samples of Tadjourah, Oga (Stn M), Shimoda (Stn N) and Darnley Island (type series of *Dentalium laeve* Brazier; "rough" and "smooth" tubes analysed separately); interior and exterior diameters of tube mouth (orifice) and apex, maximal width, length (measured in straight line between apex and orifice), length from apical width of 0.8 mm to orifice (to avoid effects of missing apices), and from height (defined as the widest distance between inner curve of tube and the straight line between apex and orifice). Various ratios have been computed, notably the arcuation (height: length $x$ 100, c.f. Palmer, 1979:739). The data were filtered for evidently incomplete tubes, and for tubes with a maximal width of less than 50% of the largest specimen from the sample. In some localities only larger tubes were measured, in this case unfiltered and filtered data are the same. After analysis of the results of these four samples only length, maximal width and height were noted for the tubes of the remaining samples.

The following abbreviations have been used in the text: AM — Australian Museum, Sydney; BMNH — British Museum (Natural History), London; ITZ — Instituut voor Taxonomische Zoölogie, Amsterdam; MNHN — Muséum National d'Histoire Naturelle, Paris; MPW — Muzeum Przyrodnicze, Wroclaw; NSMT — National Science Museum, Tokyo; RMNH — Rijksmuseum van Natuurlijke Historie, Leiden; tH — collection number in ZMA; W — short for collection number AM W; ZMA — Zoölogisch Museum, Instituut voor Taxonomische Zoölogie, Amsterdam; ZMB — Zoölogisches Museum, Berlin; ZMK — Zoologisk Museum, Kjobenhavn; ZSI — Zoological Survey of India, Calcutta.

## Taxonomic Account

### *Ditrupa* Berkeley, 1835

**Type species.** *Dentalium subulatum* Deshayes, 1825 = *Dentalium arietinum* O.F. Müller, 1776; designated by Bush, 1905 (following synonymy of Saint-Joseph, 1898).

**Diagnosis** (emended). Tube free, not attached to substratum, elongated curved fusiform, circular in cross-section. Tube open at both sides, broadening anteriorly though exterior tapers just prior to tube mouth. Tube wall consisting of variably hyaline outer and opaque

inner layer. Operculum hemispherical with chitinous end-plate. Peduncle positioned as first radiole; smooth. No pseudo-operculum. Branchial radioles arranged in two half circles, inserted on pectinate basis. Pair of filiform mouthpalps adjacent to dorsal lip. Large entire collar continuous with thoracic membranes, ending at first setiger. Six thoracic setigers, all with setae and uncini. Thoracic setae limbate and capillary, first setiger sometimes with special setae. Uncini saw/rasp-shaped (Fig. 61) or rasp-shaped (Fig. 60) with bifurcate peg; 20–30 teeth visible in profile. Abdominal setae geniculate; uncini rasp-shaped, with up to 8 rows of teeth, 20–25 in profile.

**Remarks.** *Genus. Ditrupa* was proposed as a new genus by Berkeley (1835:425–426) for two species he identified as *Dentalium subulatum* Deshayes, 1825 and *Dentalium gadus* Montagu (= *Dentalium coarctatum* Lamarck). No type species was designated.

The type locality of *Dentalium subulatum* is not known. Berkeley's Irish material, also figured by Chenu (1842–1845, Livr. 7, pl.6 fig.25; Livr. 8, pl.7 fig.13, was considered a synonym of *Ditrupa arietina* (= *Dentalium arietinum* O.F. Müller, 1776) by Sars (1851:204). This synonymy was subsequently accepted by, for instance, Saint-Joseph (1898:444) and Bush (1905:223), the latter first designated *Ditrupa arietina* (= *Dentalium subulatum*) as the type species of the genus *Ditrupa*.

Lommerzheim (1979:143) considers that the earliest name for the type species is *Dentalium corneum* Linnaeus, 1767 but the status of that name and the species it applies to is unclear, as fully discussed later in this paper.

Berkeley included *Dentalium gadus* Montagu (=*Dentalium coarctatum* Lamarck) in *Ditrupa* as well. Both names have a confused and confusing history. Montagu (1803:496) mentions *Dentalium gadus* from "...many parts of the British channel...known to mariners by the name of Hake's tooth..." Although the description and figure evidently apply to the scaphopod *Cadulus* (*Gadila*) *gadus* (Montagu, 1803), Jeffreys (1877:157) had already surmised from the locality and common name that Montagu's material at least partly belonged to the serpulid *Ditrupa arietina* O.F. Müller, 1776. As for *Dentalium coarctatum*, the name was used first by Brocchi (1814:264, pl.1 fig.4) for a fossil from south Italy with is considered to belong to *Ditrupa* by, for instance, Pilsbry & Sharp (1898:242), Wrigley (1951:191) and Ronchetti (1952:5). However, *Dentalium coarctatum* :Lamarck (1818:346) was referred to the scaphopod *Dischides bifissus* by Jeffreys (1877:157), correctly so judging from the figures by Chenu (1842–1845:livr.7, pl.6 figs 26, 36). *Dentalium coarctatum* :Philippi (1844:208) and :Costa (1850:38–39) are considered to be scaphopods of the genus *Cadulus* by Pilsbry & Sharp (1898:144,237).

*Thorax.* In almost all Sabellida the first setiger has only collar setae, all other thoracic setigers have setae and uncini. It would appear that uncini secondarily are lost in the collar segment, "setae + uncini" being the normal character state (the biramous condition occurs in both the Polychaeta and Oligochaeta). The fact that the first setiger in *Ditrupa* shows setae + uncini might thus be explained as a plesiomorphic character. However, it is generally assumed in the literature (e.g. Saint-Joseph, 1898:445; Zibrowius, 1868a:170; Bianchi, 1981:123–124) that this is not the case, but that the collar setae have become lost in *Ditrupa*. Reasons for this assumption are not given in the literature. Probably they are implicit: a pair of excretory organs are depicted anterior to the first setiger by Saint-Joseph (1898:445, fig.251). Since these occur along with collar setae in the first segment of other serpulids, he may have assumed that the collar setae are lost. Even in tiny specimens (2–4 mm), Zibrowius (1968b:384) was unable to find traces of collar setae. Nevertheless, secondary loss of collar setae, reported to occur incidentally in *Pomatoceros*, *Spirobranchus* and *Sclerostyla* (ten Hove, 1970:221; 1973:4,10) is the most likely explanation for the characteristic arrangement of the first setiger in *Ditrupa*. Thus *Ditrupa* would be apomorphic on two counts: first, loss of collar setae and, second, takeover of their function by the second setiger. In the other examples given, loss of collar setae is not accompanied by visible compensatory changes. *Placostegus*, also without collar setae, shows a belt of eyespots in the first segment; its broadly rasp-shaped thoracic uncini and short geniculate abdominal setae differ greatly from those of *Ditrupa*. Moreover, the tube structure, though hyaline, is completely different (ten Hove & Zibrowius, 1986:fig.5; Zibrowius & ten Hove, 1987:fig.3).

*Relations with other genera.* The relation of *Ditrupa* to other serpulid genera is very unclear. Grube (1862:63) placed it in *Placostegus* Philippi, 1844, solely upon the similarity in operculum. Mörch's (1863:424) literature based discussions concentrated upon the question whether the branchial radioles have one or two rows of pinnulae, and on the large collar of *Ditrupa*. However, all serpulids have two rows of pinnules, and the extent of the collar varies according to species. Mörch also alluded to a variety of *Placostegus*, which would indicate that one and the same species can live both in adnascent and free tubes ("...en Antydning til at en og samme Art kan leve baade fastheftet og frit.") Although *Placostegus* species indeed tend to grow perpendicular to the substrate, and break off easily, free living specimens have never since been mentioned in the literature. It certainly cannot be used to infer a relation with *Ditrupa*. All three arguments are moot.

*Serpula crenata* (Ehlers, 1908), widely differing in morphology from *Ditrupa*, is reported to also have curved free tubes, though angular in cross-setion. *Hyalopomatus*, also occurring in bathyal environments, very often shows a small area of attachment before growing away from the substrate. It is likely that *S. crenata* starts similarly, becoming detached in later life. It seems probably that curved tubes are an adaption to a soft sediment existence and, therefore, convergent amongst these three genera. This is probably also the case for the fossil subgenera *Triditrupa*, *Tetraditrupa* and *Pentaditrupa* as discerned by Regenhardt (1961:72–75), which do not appear to be related to *Ditrupa* at all, but more likely to a secondarily free living form like *S. crenata*.

*Ditrupa* associates, either artificially or by implication, with a number of genera in keys. Bush's (1905:221–223) key links *Ditrupa* with *Vermiliopsis* s.l. on the basis of its

operculum with chitinous endplate and the erroneous assumption that *Ditrupa* should have limbate collar setae. A chitinous endplate is widely spread in serpulids, and cannot be used for phylogenetic decisions on this level. In the keys of Southward (1963:585–587) and Fauchald (1977: 141–142), *Ditrupa* associates with *Bonhourella* (see synonymy), *Placostegus* (see above), *Sclerostyla* Mörch, 1863 (those missing collar setae only), *Dasynema* Saint-Joseph, 1894 (on the mistake that this genus lacks collar setae) and *Marifugia* Absolon & Hrabe, 1930. *Marifugia* indeed shows a superficial resemblance (no collar setae, limbate thoracic setae, uncini with gouged peg), however, it has an adnascent tube and occurs in freshwater caves. Moreover, *Marifugia* has only eight teeth per thoracic uncinus and long abdominal setae which are geniculate like those in *Vermiliopsis* s.l. (ten Hove, unpublished).

In the present state of knowledge it is not possible to attribute *Ditrupa* to one of the recognised groups such as *Pomatoceros/Spirobranchus* or *Serpula/Crucigera/ Hydroides*.

### *Ditrupa arietina* (O.F. Müller, 1776)

*Dentalium arietinum* O.F. Müller, 1776: 236. Diagnosis – Denmark and/or Norway.

*Dentalium corneum* (non Linnaeus) Lamarck, 1818: 345. Diagnosis – material studied.

p.p. *Dentalium strangulatum* Deshayes, 1825: 372–373. Diagnosis – one syntype studied, see nomenclature of *Ditrupa gracillima*.

*Dentalium subulatum* Deshayes, 1825: 373, pl.16 fig.29. Diagnosis – unknown locality.

*Ditrupa subulata*.—Berkeley, 1835: 424, pl.19 fig.2. Diagnosis – Ireland.—Chenu, 1842–1845: livr.7, pl.6 fig.25; livr.8, pl.7 fig.13. Diagnosis – Ireland.

*Serpula libera* Sars, 1835: 52–54, pl.12 fig.33. Description – Norway.

*Ditrupa arietina*.—Sars, 1851: 204. Name only.—Saint-Joseph, 1898: 443–447, pl.23 figs 249–254. Description – Gulf of Biscay.—Fauvel & Rullier, 1959: 196 (in part; their specimen from Rio de Oro is D. arietina, the other two specimens are scaphopods. Material studied MHNH; also fide Zibrowius, 1973:78–79).—Zibrowius, 1968a: 169–171, pl.9 figs 8–13. Description – Mediterranean Sea.—Zibrowius, 1968b: 383–385. Diagnosis – material studied.—Bianchi, 1981: 124–125, fig.47. Diagnosis – Italy.

*Dentalium goreanum* Clessin, 1896: 42, pl.10 figs 9–10. Description of tube – Senegal.

*Ditrypa arietina*.—Bush, 1905: 223. Name only.—McIntosh, 1923: 380–383, pl.122 figs 5–6, pl.132 fig.1. Description, discussion – U.K., Azores, Mediterranean.

**Material studied.** ICELAND – off south Iceland, coll. R.E. Stobbs (1 tube, AM W201218). NORWAY – Bergen (3 mounted tubes, older label *Serpula libera* Sars. UNITED KINGDOM – off Flamborough Head, *UK 68*, 29 Jan. 1987 (1 specimen, private collection E. de Wit). FRANCE – "*Travailleur* stn 111, 9 Aug. 1882, 100 m" (33 tubes, MHNH; label not conform list of localities of the "*Travailleur* according to note by Zibrowius); Mediterranean, Baie de Cavalaire, coll. Bodoy, 1980, 40-50 m (50 tubes, ZMA tH 500). MOROCCO – Atlantic, 33°30'N, 08°24'W, stn 56, *Vanneau*, 24 June 1924 (32 specimens, MNHN). MADEIRA – Lapa Island, stn 10 *Jean Charcot*, 12 July 1966 (10 specimens ZMA tH 69); Funchal, coll. Sjorensen (2 tubes, ZMK); west of Deserta Grande, 32°29'N, 16°31'-32'W, stn 19, 21 *Onversaagd*, 8 Mar. 1976 (2 specimens from 30 m, 100 tubes from 240 m, ZMA tH 560/1). CANARY ISLANDS – south-west off Palma 28°39'N, 17°58'W, stn 4.148 RV *Tydemann*, 3 June 1980, 60-80 m (10 specimens, 100 tubes, ZMA tH 559). RIO DE ORO – Cap Blanc, 21°05'N, 17°14'W, stn 1, *Calypso*, 10 May 1956 (1 tube, MNHN).

**Diagnosis.** *Tube*. The tube (Figs 19–21,23) is tusk-shaped and slender, open at both ends, with a length of up to 34 mm (usually 25–32 mm). Generally tubes appear to be whitish, mottled with brown even after 150 years in collection; however, this colouration of the inner tube layer may vary according to population. The outer tube layer is hyaline, unless it is opaque by abrasion. Irregularities in tube wall thickness may cause 'annuli' (e.g. figs 9–10 of *Dentalium goreanum* Clessin, 1896: 42; Fig.23). However, these annuli never are so abruptly and regularly elevated as in the "monilifera" forms of *Ditrupa gracillima*.

| | Maximum tube width | Arcuation index |
|---|---|---|
| Cavalaire | 1.9-**2.32**-2.7 (SD = 0.24) | 10.5-**12.8**-15.0 (SD = 1.7) |
| all material | 1.5-**2.16**-2.8 (SD = 0.33) | 10.5-**13.5**-17.1 (SD=2.0) |

For explanation see *D. gracillima*.

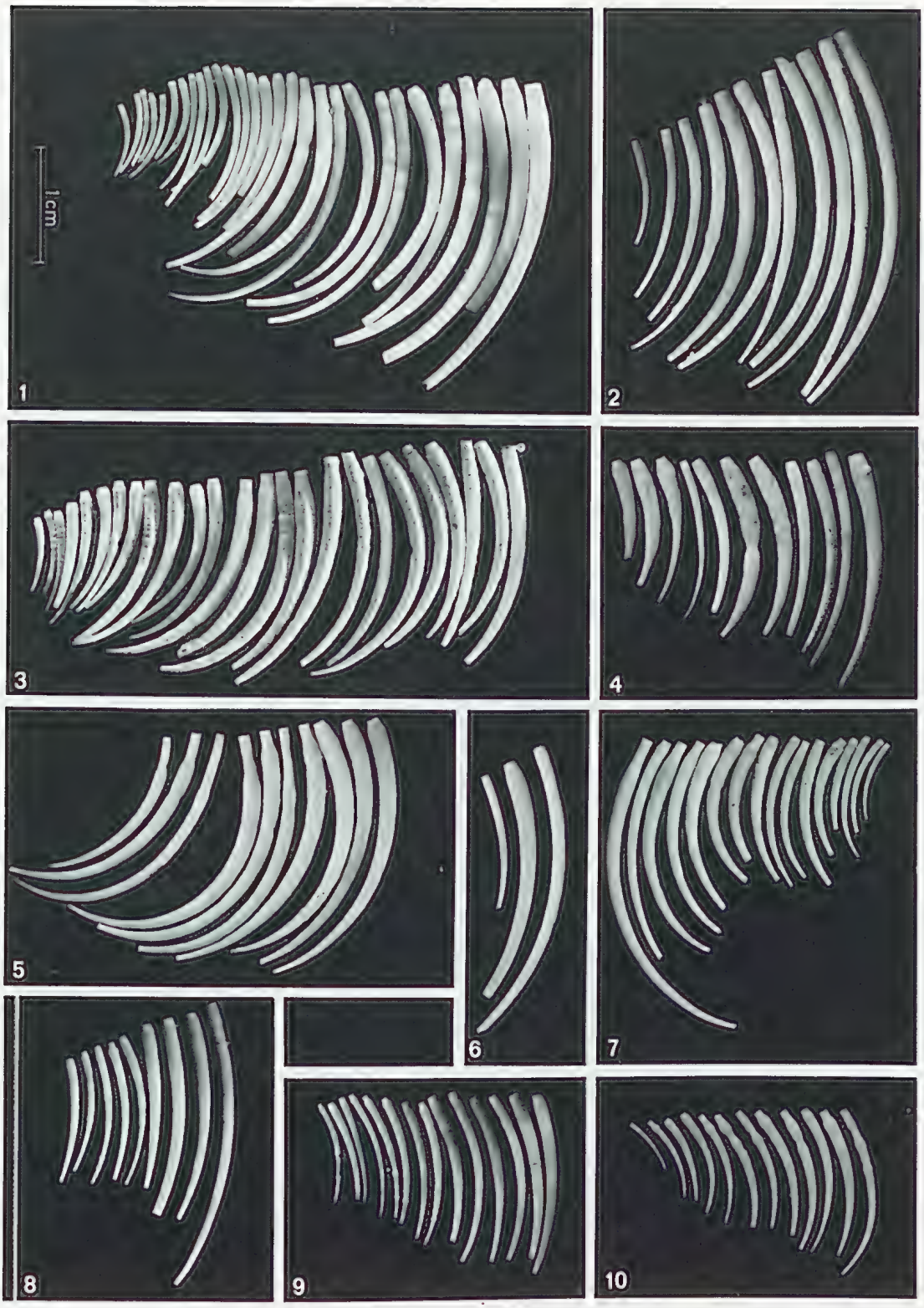
*Branchiae and peduncle*. Generally 10–12 pairs of branchial radioles. See further *D. gracillima*.

*Operculum*. Globular, with a distal chitinous endplate. Endplate flat and circular, usually featureless. Rarely a small central spine, surrounded by a few concentric growth-rings. Globular ampulla has form of an inverted cone. We have not been able to find a talon to the opercular plate, as figured by Nelson-Smith & Gee (1966:fig.13B). At most there is a faint depression of the chitinous endplate. Diameter of operculum up to 1.2 mm, length of ampulla up to 1.3 mm.

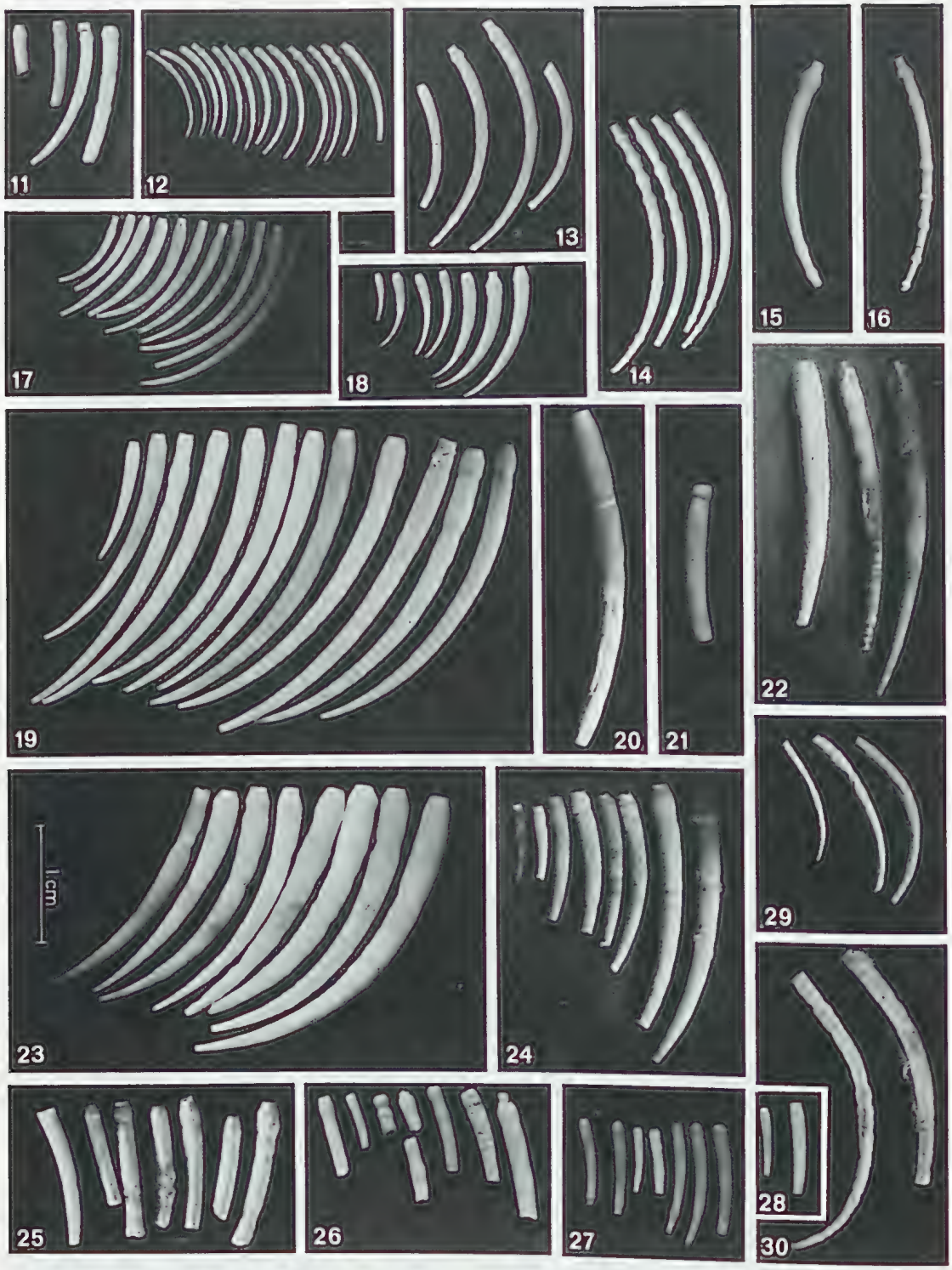
*Collar and thoracic membranes*. Collar well developed, with entire edge. Bianchi (1981:123–124) mistook the slightly swollen sides of the thorax for a continuation of the thoracic membranes. Contrary to his opinion and fig.47b, there is no apron across the abdomen, but thoracic membranes end just anterior to the first setiger.

*Setation*. Thorax has only 6 setigers, rather than the 7 usual in other serpulids, and all are uncinigerous. Collar setae absent. First setiger occupies a place similar to that of collar setiger in other serpulids, is widely spaced from remaining 5 setigers. All thoracic setae, including those of first setiger, are limbate and of two sizes (checked in 25 specimens from 3 localities). Uncini along entire thorax saw- to rasp-shaped for their greater parts but with 2 or 3 rows of 2–3 teeth just above anterior fang. Up to 22 teeth can be seen in profile.

The up to 55 abdominal setigers have all rasp-shaped uncini. The posterior 20–25 setigers may have a few almost capillary setae as well, with faintly geniculate tips.




**Figs 1—10.** For full details of localities see text. *Ditrupa gracillima* — 1: Queensland, Darnley Island, smooth tubes; lectotype of *Dentalium laeve* Brazier is 20th specimen from left; juvenile tubes with up to 4 annuli; 2: Japan, Shimoda, tubes 3,6 and 8 are rough or smooth to rough; 3: Queensland, Darnley Island, rough and smooth to rough (6,13,14 from left) tubes; 4: La Réunion (170–225 m), variation in roughness and expansion rate; 5: Gulf of Tadjoura, variation in expansion rate and arc, extended orifices; 6: syntypes of *D. gracillima*; 7: Papua, Manubada, tubes 4 and 7 are rough-smooth-rough; 8: La Réunion (45 m), up to 4 annuli; 9: La Réunion (75–90 m), smooth and rough tubes, up to 5 annuli; 10: Western Australia, Bunbury, irregular growth patterns but no real annuli. All approximately (10% error) to same scale.




**Figs 11—30.** For full details of localities see text. *Ditrupa gracillima* — 11: New South Wales, Sydney, up to 3 annuli; 12: Western Australia, Dampier, monilifera-forms, but also 1 tube with a single annulus; 13: Iranian Gulf, Patrick Stewart Bank, up to 3 annuli; 14: Solomon Islands, monilifera-forms with 4–7 annuli; 15: New South Wales, Cape Three Points; 16: Indonesia, Great Kei, monilifera-form; 17: Red Sea, Menar Aba Samra, smooth to/and rough tubes; 18: Indonesia, Kalimantan, high expansion rate. *Ditrupa arietina* — 19: Marseille; 20: off South Iceland, with abnormal longitudinal depression; 21: syntypes of *Dentalium strangulatum*; 23: France, stn 111. *Ditrupa aff. arietina* — 22: Pleistocene, Italy, Torrente Stirone (W 201219); 24: Pliocene, Italy, Bodognano (W 201238). *Ditrupa strangulata* — 25: Eocene, France, Basin of Paris, Belleu (ZMA tH 115). *Ditrupa gracillima* — 26: Miocene, Victoria, Rutledge Creek; 27: Miocene, Victoria, Hamilton, some tubes with annulus; 28: Miocene, New Zealand. *Serpula crenata* — 29,30: New South Wales, off Eden (W 201245). All approximately (10% error) to same scale.

*Ecology*. Although tubes have been collected from depths down to 530 m, specimens are known only to a depth of 150 m.

**Remarks.** Sars (1835) described the animal as a new species *Serpula libera*, since *Dentalium arietinum* Müller was based on an empty shell only. In 1851 he placed his own species into the synonymy of *Ditrupa arietina*, the older available name. A full revision of the species, which has been mentioned in the literature well over a hundred times under at least ten specific names falls outside the scope of present paper.

**Distribution.** Boreal to subtropical: East Atlantic from Iceland to Azores, Canary Islands and Senegal; Mediterranean and ?Black Sea.

### *Ditrupa gracillima* Grube, 1878

?p.p. *Dentalium strangulatum* Deshayes, 1825 (1826?): 372–373, pl.16 fig.28. Diagnosis – not the fossils from Europe, but the recent material from "Terres Australes", see Nomenclature.

?p.p. *Ditrypa strangulata*.—Mörch, 1863: 426. Diagnosis – Terres Australes.

*Dentalium laeve* (non Turton, nec Schlotheim) Brazier, 1877: 59. Diagnosis – north-east Australia, material studied, AM A 93, i-iii, C.7523, a, C.2528.—Ponder & Stanbury, 1972: 53. Lectotype in Macleay Museum, presently deposited in the AM. See Nomenclature.

*Ditrypa gracillima* Grube, 1878: 279–280. Description – Philippines.—Wiktor, 1980: 281. Type in MPW, nr.272.

*Cadulus laevis*.—Pilsbry & Sharp, 1898: 195. No new data, although they doubt if the species is a scaphopod.—Hedley, 1900: 499, pl.26 figs 8–10. Diagnosis after types.—Boissevain, 1906: 75–76, pl.3 fig.43. No new data.—?Cotton & Godfrey, 1933: 149. Diagnosis – south-west of Neptune Islands, SA.

*Bonhourella insignis* Gravier, 1905: 448–451. Description – Djibouti, Golfe de Tadjourah, 20 m.—Gravier, 1906: 115 (name only).—Gravier, 1906-1908: 134–138, figs 493–495, pl.8 figs 301–302. Description – Djibouti, Golfe de Tadjourah, 20 m. See Remarks.

*Ditrupa arietina* (non Müller) Gravier, 1906: 113 (Name only). Djibouti, 15–20 m, material studied MNHN.—Gravier, 1906–1908: 124–125. Description – Djibouti, 15–20 m, material studied MNHN.—Fauvel, 1932: 247. Description – Andaman Sea, 1500 m; see Introduction.—Fauvel, 1933a: 80 (name only). Gulf of Eilat, Suez.—Fauvel, 1933b (name only). Gulf of Eilat, Suez.—Monro, 1937: 319 (name only, but referring to var. *monilifera* for Aden material). Red Sea, South Arabian Coast, 26–38 m, Gulf of Aden, 655–732 m, material partly studied.—Mesnil & Fauvel, 1939: 36 (name only). Salibabu Island, material studied, ZMA V Pol 1639.—Wesenberg-Lund, 1949: 358 (name only). Iranian Gulf, 50–60 m, material studied ZMK.—Fauvel, 1953: 470, figs 246a–g. Andaman Sea, 1500 m. [N.B. The figures are a copy of Fauvel, 1927 and referring to Mediterranean material].—p.p. Zibrowius, 1973: 78 (name only). Malagasy, Djibouti, material from last locality studied, MNHN.—Imajima, 1978: 69 (name only). Izu Islands, Japan, up to 85 m.—Imajima, 1979 (name only). Honshu, Japan, part of material studied, ZMA tH 383.—Imajima, 1982: 53 (name only). Palau Islands, 5 m, part of material studied, ZMA tH 458.—Soota, Misra & Chakraborty, 1980: 69. Material studied, ZSI.—Hong, 1984: 42–46, fig.4a–m. Description – South Korea.—Vine & Bailey-Brock, 1984: 146 (name only). Red Sea, 75–80 m.

?*Ditrypa australia* Bretnall, 1921: 156, fig.2. Description – holotype not found in AM in 1986.—Dew, 1959: 47, fig.18A. Diagnosis – Queensland, New South Wales, 2–20 m. Material not found in AM.—Straughan, 1967: 248 (no new data). see Remarks.

*Ditrypa brazieri* Bretnall, 1921: 156, fig.1. New name for *Dentalium laeve* Brazier, of which the holotype is in the Macleay Museum, University of Sydney.

*Ditrupa arietina* var. *monilifera* Fauvel, 1932: 247, fig.12. Diagnosis – Andaman Sea, 642 m, material studied ZSI.—Mesnil & Fauvel, 1939: 36. Diagnosis – Kei Island, material studied ZMA V Pol 1634.—Fauvel, 1953: 470, fig.246h. Andaman Sea, 642 m, material studied ZSI.—Soota, Misra & Chakraborty, 1980: 69. Material studied ZSI.

*not Ditrupa crenata* (Ehlers).—Mesnil & Fauvel, 1939: 36. Indonesia. This species belongs to the genus *Serpula* s.l., material studied ZMA V Pol 1640, 1739. It also is known as *Dentalium tiwhana* Dell (1953: 48, figs 17–22; 1957: 564, figs 17–19, pl.39 figs 6–7) part of material studied, AM W 201251.

*Ditrupa amphora* Dew, 1959: 48, fig.18D. Diagnosis – Queensland, 150 m; material not found in AM.

*Ditrupa laeve*.—Dew, 1959: 47, figs 18B,C. Diagnosis – Queensland, 100 m, material not found in AM.

*Ditrupa arietina monilifera*.—Hartman, 1974: 200 (name only). Bay of Bengal off Kakinada, 37 m.

**Material studied** (unless stated otherwise the tubes are "smooth"; "monilifera" forms are indicated by *). La Réunion — 19°44'-21°20'S, 54°08'-55°52'E, *Marion Dufresne* campagne MD32, 12 Aug. 1982 - 2 Sept. 1982, 40-980 m, stn DC 1, 3, 10, 41, 56, 86* (75-90 m), 124, 126* (110 m), 128, 176, FA 39, DR 90, 154 (altogether 500 tubes of which 40 "rough", 7 specimens: MNHN, ZMA tH 617, 618, W 202505/6, USNM 104939/40). Madagascar — south-west Madagascar, région de Tuléar: Andeteky, S.Grand Récif, Ankarandara, Lagon de Tuléar, coll. B.Thomassin, J.Picard *et al.* – stn 222, 29 Sept. 1969, 24 m (1 spec., 1 rough and 1 smooth tube); 227, 2 Oct. 1969, 27 m (1 spec., 7 tubes); 231, 236, 240, 3-8 Oct. 1969, 15-36 m (1 spec., 13 tubes of which 8 rough); 617, 621, 622, 623, 9-11 Apr. 1972 (2 specs, 24 tubes of which 11 rough); 658, 28 Oct. 1971, 112 m (8 tubes); 726, 730, 734, 737, 738, 741, 20-25 May 1972, 12 m (64 tubes, of which 12 rough); 1305, 1307, 1316, 1321, 1330, 1340, 1341, 1351, 1352, 1354, 28 Aug. 1963 - 25 Sept. 1963, 10-77 m (4 specs, 50 tubes of which 6 rough); 1336, 12 Sept. 1963, 280 m (1 tube). Most specimens MNHN; some ZMA tH 619, W 202504 and USNM 104938. Comores — Campagne BENTHEDI Mayotte, Sud îlot Gombé Doumé, 12°45'S, 45°15.9'E, stn 18S, 22 Mar. 1977, 15 m (2 specs, MNHN); W de la Grande Passe de l'Ouest, 12°46'S, 44°57.6'E, stn 62DS, 29 Mar. 1977, 530-535 m (59 tubes*, some living, MNHN, ZMA tH 613); Sud Banc de la Zélée, 12°25.6'S, 46°16.2'E, stn 110S, 10 Apr. 1977, 24m (1 tube, MNHN). Gulf of Tadjoura — between

Pingouin and Météore Reefs, coll. Gravier, 26 Feb. 1904 - 22 Mar. 1904, 15-20 m (30 specs, 80 tubes, MNHN and ZMA tH 598). RED SEA — stn. MB 1d, coll. John Murray Expedition, 17 Sept. 1933, 26 m (1 spec., 2 rough tubes, BMNH ZK 1937.9.2.582); Gulf of Aqaba – stn. 38, coll.R.Ph.Dolfuss, 1 Feb. 1929 (7 tubes, MNHN); Nuweiba, coll. J.Levy, Apr. 1977, coral sand, 18 m (1 tube, W 201228); off West Murach, stn. 36, 9 Oct. 1976, 73-82 m (15 tubes, W 201258); off Nuweiba el Tarabin, stn 34, 8 Oct. 1969, 137-146 m (2 tubes, W 201248); off Menar Aba Samra, stn 3, 6 Oct. 1969, 46-49 m (75 rough and smooth tubes, W 201296); off Mersat Abu Samra (north), stn 4, 6 Oct. 1969, 51-53 m (35 rough and smooth tubes, W 201254); same (centre), stn 5, 6 Oct. 1969, 49-55 m (13 rough and smooth tubes, W 201294); Eilat, stn 8, coll. C.Lewinsohn, 7 Sept. 1966, 60-80 m (10 tubes, W 201304); marine station, stn AQ4, coll. B.A.Thomassin, 17 Apr. 1981, 10 m (1 spec., MNHN). SOUTH ARABIAN COAST — stn 43, 45, coll. John Murray Expedition, 28-29 Oct. 1933, 40-83 m (3 incomplete specs, 16 rough and smooth tubes, BMNH ZK 1937.9.2.581,585-589). GULF OF OMAN — stn 72, coll. John Murray Expedition, 26 Nov. 1933, 75 m (40 tubes, BMNH ZK 1937.9.2.590). IRANIAN GULF — 7 miles east-north-east of Patrick Stewart Bank, *Ingolf* stn 71D, coll. G.Thorson, 19 Apr. 1937, 69 m (3 tubes, ZMK); 29°04'N, 49°56'E, *Ingolf* stn 23D, coll. G.Thorson, 13 Mar. 1937, 50 m (1 tube, ZMK); 26°33'N, 56°42'E, stn 94, coll. Blegvad, 28 Mar. 1938 (1 tube, ZMK). ANDAMAN SEA — 11°26'30"N, 92°53'45"E, *Investigator* stn 322, 378 fms (1 specimen*, TYPE of var. *monilifera*, ZSI). SRI LANKA — north of Trincomalee, 8°54.5'N, 81°05.5'E, stn 260, coll. M.V.*Survey*, 12 Aug. 1921, 29 m (6 tubes of which one rough, W 201259); 9°16'N, 79°28.5'E, stn 390, coll. M.V.*Survey*, 19 Sept. 1921, 13 m (1 tube, W 201250), Palk Strait, 9°57.5'N, 79°46'E, stn 358, coll. M.V.*Survey*, 16 Sept. 1929, 13 m (1 tube, W 201234); 12 miles south of Galle, stn 187a, 27 Dec. 1920, 91 m (1 tube, W201285). SINGAPORE — east of Singapore, 1°45'N, 106°40'E, coll. Andréa, 1869, 63 m (2 tubes, ZMK). THAILAND — Gulf of Thailand, off Koh Mok, Koh Kut and Koh Chuen, coll. Th. Mortensen, Jan. - Mar. 1900, 18-36 m (4 tubes, ZMK). HONG KONG — east side of Mirs Bay, south-east of Ping Chau Island, coll. A.J. Brandt & W.F. Ponder, 12 Nov. 1973, sand deposits from dredging, to 8 m (10 tubes, W201231). KOREAN STRAITS — west of Goto Islands, 33°02.5'N, 128°48.5'E, stn 11, HMS *Sylvia*, coll. Capt. St. John, 1876, 40 m (2 specs in smooth tubes, 1 rough tube BMNH ZH 1878.10.25.2); 33°14'N, 128°55'E, probably stn 17, HMS *Sylvia*, coll. Capt. St. John, May 1876, with *Spirobranchus latiscapus* (Marenzeller, 1885), 72 m (1 tube, BMNH ZB 1977.102). JAPAN – Sea of Japan, 130 m (2 dried out specs in rough and smooth tube, BMNH ZK 1921.5.1.4513); Honshu, Sea of Japan, off Oga, 13 localities between 39°48'-40°06'N and 139°41'-53'E, 31-101 m (200+ specimens); off Akita, 39°47'N, 139°51'E, 60 m (1 spec.). Honshu, Pacific Ocean, Sagami Nada, 35°09'N, 139°23'E, 500 m (1 spec.); Suno-Saki, coll. Th. Mortensen, 12 June 1914, 36-144 m (3 tubes, ZMK); off Shimoda, 18 localities between 34°37'-45'N and 138°56'-139°02'E, 39-120 m (150+ specimens). All specimens (except ZMK) ident. M.Imajima, *D. arietina*, NSMT, ZMA tH 608, 609; off Kushimoto, coll. M. Imajima, July 1978, 58-60 m (2 specs, rough tubes, ZMA tH 383). PALAU ISLANDS – Arumonogui, coll. M.Imajima, July 1980 (2 specs, ZMA tH 458). PHILIPPINES – Pandanon, coll. Semper (SYNTYPES, 1 incomplete, partly macerated specimen and 3 tubes, MPW 272; 2 incomplete specimens with tubes, ZMB 1560); 11°42.6'N, 122°34.5'E, stn 140, campagne MUSORSTOM 3, 6 June 1985, 99-93 m (3 tubes, MNHN); off Jolo, coll. Th. Mortensen, 20 Mar. 1914, 38 m (1 spec., ZMK). INDONESIA — Kalimantan (=Borneo; 7 tubes, W 201226); off Java, 8°S, 114°E, stns 6, 9, coll. Th. Mortensen, 5-6 Apr. 1929 (30 tubes, ZMK); Salibabu Island, anchorage off Lirung, Siboga stn 133, 25/27 July, 1899, mud and hard sand, to 36 m (1 rough tube, ZMA V.Pol.1639); Ambon Bay, off Kota Ambon, 3°42'S, 128°10'E, Snellius II Expedition, stn 4.008, 4 Apr. 1984, sandy, 105 m (1 tube, RMNH 18173); Amboina, leg. Semon (2 tubes, ZMB F412); Kei Island, off Toeal, stn 19, coll. Th. Mortensen, 14 Apr. 1922, 20 m (1 rough tube, ZMK); west of Great Kei Island, 5°53.8'S, 132°48.8'E, *Siboga* stn 262, 18 Dec. 1899, solid bluish grey mud, 560 m (1 tube*, ZMA V.Pol.1634). PAPUA — off Port Moresby, on sheltered north-west side of Manubada (Local) Island, coll. W.F. Ponder & P.H. Colman, 21 June 1970, in sticky sandy mud, 23 m (1 rough to smooth tube, W 201275); same, west end of Manubada (Local) Island, coll. W.F. Ponder & P.H. Colman, 24 June 1970, just inside outer reef, sticky muddy sand, 18-22 m (180 tubes of which 35 rough or partly rough, W 201220, ZMA tH 607); south-west Port Moresby, off west side of Lolorua Island, coll. W.F. Ponder & P.H. Colman, 21 June 1970, 13-18 m (9 rough tubes, W201263); off Cape Possession, near Yule Island, Gulf of Papua, coll. P.H. Colman, 12 Nov. 1970, 27 m (1 tube, W 201242). NEW CALEDONIA — 21°35.8'S, 166°29'E, stn DW106, campagne BIOCAL, 8 Sept. 1985, 650-625 m (2 specs*, MNHN, ZMA tH 612). SOLOMON ISLANDS — west coast Malaita Island, off Laulesi, coll. P.H. Colman, 27 Aug. 1973, olive-grey mud and stones, 366 m (4 tubes* with dry specimens inside, W 201290). AUSTRALIA — Western Australia: east of Hood Point, CSIRO, stn G2/109/62, HMAS *Gascoyne*, 82 m (8 tubes, W 201269); east off Cheyne Bay, 34°55'S, 119°00'E, CSIRO, stn G3/150/62, HMAS *Gascoyne*, 7 Aug. 1962, 75 m (6 tubes, W 201267); between Port Augusta and Cape Leeuwin, 34°40'-32'S, 114°56'-115°02'E, stn G3/170-171/62, HMAS *Gascoyne*, 9 Aug. 1962, 66-130 m (1 tube, W 201298); south-west of Cape Naturaliste 33°44.5'S, 114°26.1'E, stn 21, HMAS *Diamantina*, 16 Mar. 1972, 238-183 m (1 tube, W 201222); west of Bunbury, 33°03'S, 114°44'E, CSIRO, stn G3/175/62, HMAS *Gascoyne*, 10 Aug. 1962, 156 m (150 tubes, W 201207, ZMA tH 608); Houtman's Abrolhos, south of Pelsart Island, 29°06.7'-07.5'S, 113°58.5'-114°00'E, stn 33m, M.V. *Sprightly*, 91.4 m (1 rough tube, W 201230); 50 miles north of Boolbarly, 23°28'S, 113°28'E, CSIRO, 18 Nov. 1948, cone dredge, 91.5 m (2 tubes, W 201293); 170 miles west of Port Hedland, 19°29'S, 116°01'E, BMR stn E68-743, M.V. *Espirito Santo*, 1 Dec. 1968, 137 m (4 tubes* W 201266); 72 miles north-north-west of Dampier, 19°28.9'-29.0'S, 116°29.4'-0'E, stn 26-18, FRV *Soela*, coll. B.W. Jenkins, 26 Oct. 1983, 110 m (30 tubes*, W 201236); 120 miles north of Port Hedland, 18°42'S, 118°02'E, BMR stn E68-708, M.V. *Espirito Santo*, 25 Nov. 1968, 161 m (5 tubes, W 201221); 200 miles west of Roebuck Bay, 18°33'S, 119°08'E, BMR stn E68-554, M.V. *Espirito Santo*, 128 m (4 tubes, W 201252); 280 miles west of Roebuck Bay, 18°30'S, 118°03'E, BMR stn E68-576, M.V. *Espirito Santo*, 11 Oct. 1968, 238 m (5 tubes*, W201278). Northern Territories: Darwin, off Emery Point, coll. P.H. Colman, 25 Oct. 1969 on sandbar (1 tube, W 201284); 200 km north of Melville Island, 9°23'S, 131°22'E, BMR P69-1186, M.V. *San Pedro Sound*, coll. P.H. Colman, 15 Nov. 1969,

clayey sand, 215 m (1 tube, W 201223); 250 km north of Melville Island, 9°09'S, 131°35.5'E, BMR-1176, M.V. *San Pedro Sound*, coll. P.H. Colman, 14 Nov. 1969 (1 tube, W 201209); 91 km north of Goulburn Island, 10°42'S, 133°36'E, BMR stn 1065, M.V. *San Pedro Sound*, coll. P.H. Colman, 31 Oct. 1969, clayey sand, 58 m (2 tubes, W 201282); 210 miles north-east of Croker Island, 8°18'S, 133°58'E, M.V. *San Pedro Sound*, coll. P.H. Colman, 3 Nov. 1969, 132 m (1 tube, W 201271); 420 km north of Melville Island, 8°18'S, 134°11'E, BMR stn 1091, M.V. *San Pedro Sound*, coll. P.H. Colman, 3 Nov. 1969, sand, 141 m (1 tube*, W 201206); 365 km north of Milingimbi Island, Arnhem Land, 8°48'S, 134°58'E, BMR stn 985, M.V. *San Pedro Sound*, coll. P.H. Colman, 18 Oct. 1969, clayey sand, 100 m (5 tubes, W 201261). Queensland: coll. E.J.Gabriel (1 rough tube, BMNH ZK 1965.31.77); Gulf of Carpentaria, south of Sweers Island, coll. D.F. McMichael & party, 7/9 Dec. 1963, 9-12 m (1 tube, W 201249); Torres Strait, Darnley Island, York Island, Chevert Exp. 1875, 5-30 fms (235 tubes of which 100 rough, AM A93, A93i, C7523, C7523a, C7528); off Murray Island, 9°56'S, 144°04'E, coll. C. Hedley, 30 Aug. - 3 Oct. 1907, 9-15 m (4 smooth and rough tubes, W 201239); Cape Grenville, Chevert Expedition 1875, 20 fms (1 tube fragment, AM A93iii); Princess Charlotte Bay, Chevert Expedition 1875 and coll. C. Hedley, 24 m (16 smooth and rough tubes, AM A93ii, W 201205); Low Isles, near Port Douglas, British Great Barrier Reef Expedition, coll. Iredale, McNeill & Livingstone, Oct. - Nov. 1928 (1 tube, W 201306); off Endeavour Reef, 20 fms (25 tubes of which 23 rough, AM); off Cairns, 16°51'36"-00"S, 146°01'12"-04'E, stn C23, HMAS *Kimbla*, coll. W.F. Ponder & I. Loch, 14 Oct. 1981, sandy mud/shell, 33-35 m (4 smooth and rough tubes, W 201262); off Townsville, soft sediment bottoms, 12-36 m (numerous, W 202429/30, ZMA tH 621); same, 18°49'S, 146°58'E, stn 938, R.V. *James Kirby*, 12 Jan. 1982, 34-35 m (3 rough tubes, W 201300); west of Hayman Island, 20°03'S, 148°50'E, stn 11, HMAS *Kimbla*, coll. P.H. Colman & F. Rowe, 19 Nov. 1977, grey, muddy sand, 33 m (7 tubes, W 201229, 201255); off Mackay, 21°03'S, 149°39.2'E, stn 15, HMAS *Kimbla*, coll. W.F. Ponder, I. Loch & P. Terrill, 13 Dec. 1977, thick, fine grey mud, 37 m (1 tube, W 201265); east of Broad Sound, 21°58.5'S, 150°45'E, stn 6, HMAS *Kimbla*, coll. P.H. Colman & F. Rowe, 18 Nov. 1977, coarse to fine sandy mud and shell, 57 m (3 tubes, W 201276); east of Broad Sound, 22°06'S, 150°49'E, stn 18, HMAS *Kimbla*, coll. W.F. Ponder, I. Loch & P. Terrill. 13 Dec. 1977, coarse shell, 53 m (1 tube, W 201243); 2 miles north-east of west side of Gillett Cay, Swains Reef, Australian Museum Party, 17-19 Oct. 1962, 63-72 m (50 rough tubes, W 201235); south-east of Swains Reef, 22°31'-32'S, 152°33'-42'E, stns 8, 9, HMAS *Kimbla*, coll. P.H. Colman, 5 July 1984, 78 m (3 tubes, W 201233, +17 tubes AM); 24.5 miles east of Lady Musgrave Island, 23°33.7'S, 152°37'E, stn 3, HMAS *Kimbla*, coll. P.H. Colman & F. Rowe, 17 Nov. 1977, yellow/grey mud, 348-339 m (1 tube*, W 201232); Hervey Bay, coll. J. Voorwinde (1 tube, W 201204). New South Wales: east of Cape Three Points, 33°28'-29'S, 151°52'E, stn K79-20-08, FRV *Kapala*, coll. K.J. Graham, 5 Dec. 1979, 457-476 m (1 tube, W 201224); Port Stephens, HMS *Herald* circumnavigation, coll. Rayner & McDonald, Apr. 1857, 135-144 m (1 tube, BMNH ZH 1859.1.14.6); east of Sydney, CSIRO, HMAS *Gascoyne*, stn G2/55-57/62, 18 July 1962, 75-150 m (4 tubes, W 201286); 1.5 km south-east of Long Bay, shelf benthic survey, 20 July 1972 (2 tubes, AM).

**Fossil.** AUSTRALIA — Victoria: Warrambyne Creek, beside road bridge, about 3 miles south-west of Interleigh, coll. P. Rodda. Middle Miocene, Bairnsdalian or younger (25 tube fragments, W 201253); Rutledge Creek, to east of Port Campbell, coll. W.F. Ponder, T.A. Darragh & E.K. Yoo, 6 Mar. 1977. Middle Miocene, Bairnsdalian, Rutledges Creek. Member, Port Campbell Limestone (1000 tubefragments, W 201308/9, ZMA tH 558); Hamilton, Muddy Creek, north behind Yulecart Hall, coll. W.F. Ponder & E.K. Yoo, 3 Mar. 1977. Lower Miocene, Batesfordian, in Muddy Creek Marl, Lower Beds, just below base of Upper Beds (15 tubes partly rough, W 201227); same, south-west below Clifton Homestead, in McDonalds Bank, coll. W.F. Ponder & E.K. Yoo, 4 Mar. 1977. Pliocene, Kalimnan, Grange Burn 'Coquina', Upper Beds (1 tube, W 201288); Portland, rocky shore below Whalers Bluff, coll. W.F. Ponder & E.K. Yoo, 4 Mar. 1977. Miocene, Upper Portland Member (20 broken tubes of which 5 with orifice, W 201246). NEW ZEALAND — South Island: Pareora, south of Timaru, 1904, pres. C.Hedley, Lower Miocene (2 tubes, W 201247).

**Description.** *Tube.* The tube (Figs 1–18, 26–28, 31–37) is tusk-shaped and slender, open at both ends, with length of up to 33.7 mm (usually 20–25 mm). Although the tube surface is usually clean and bright white in living animals, there are three ways — "smooth", "rough" and "monilifera" — in which its appearance may vary. "Smooth" tubes (Figs 1,10) are characterised by a highly polished porcellaneous finish. "Monilifera" forms (Figs 14, 16) share this but also feature irregularly spaced annular thickenings along their length (they are so-called from the first specimens collected with this feature — var. *monilifera* Fauvel, 1932). Generally the outer tube layer is somewhat translucent, while the inner layer is opaque. The translucent layer is not as hyaline as in *D. arietina*, though it is very similar in ultrastructure (compare Figs 31,34 with Zibrowius & ten Hove, 1987, fig.3). About one quarter of the tubes have a surface classified as "rough" (Figs 3,4). In these, the outer layer is chalky and opaque. A fine honeycomb structure (Fig. 32) gives these tubes a somewhat coral-like appearance. Intermediates with a partly rough, partly smooth surface occur (Fig. 2,3,7). See Remarks for discussion.

Tubes broaden very gradually from posterior apex, which is entire, towards orifice. Minimal measured internal diameter of apex is 0.16 mm, which presumably is the width of a newly metamorphosed larva. Internal diameter of orifice is 0.35–1.1 mm, generally about 0.9 mm. Just before orifice, tubes narrow at a gentle angle, forming conical shoulder (Fig. 35) up to 2.4 mm in width (generally less than 2 mm, see below). In few cases part between shoulder and orifice concavely extended, like the neck of a bottle (Fig. 5). The rim of the tube mouth is circular, smooth and entire. A pronounced thickening is absent, except in a few juvenile tubes with a "monilifera" appearance (Fig. 1). Rarely a thickened orifice shows an irregular pattern of shallow indentations (Fig. 36, see Ecology).

Giving reliable statistics of tubes is extremely difficult since the apex is often missing for an indeterminable distance. Not knowing the expansion rate, which appears to

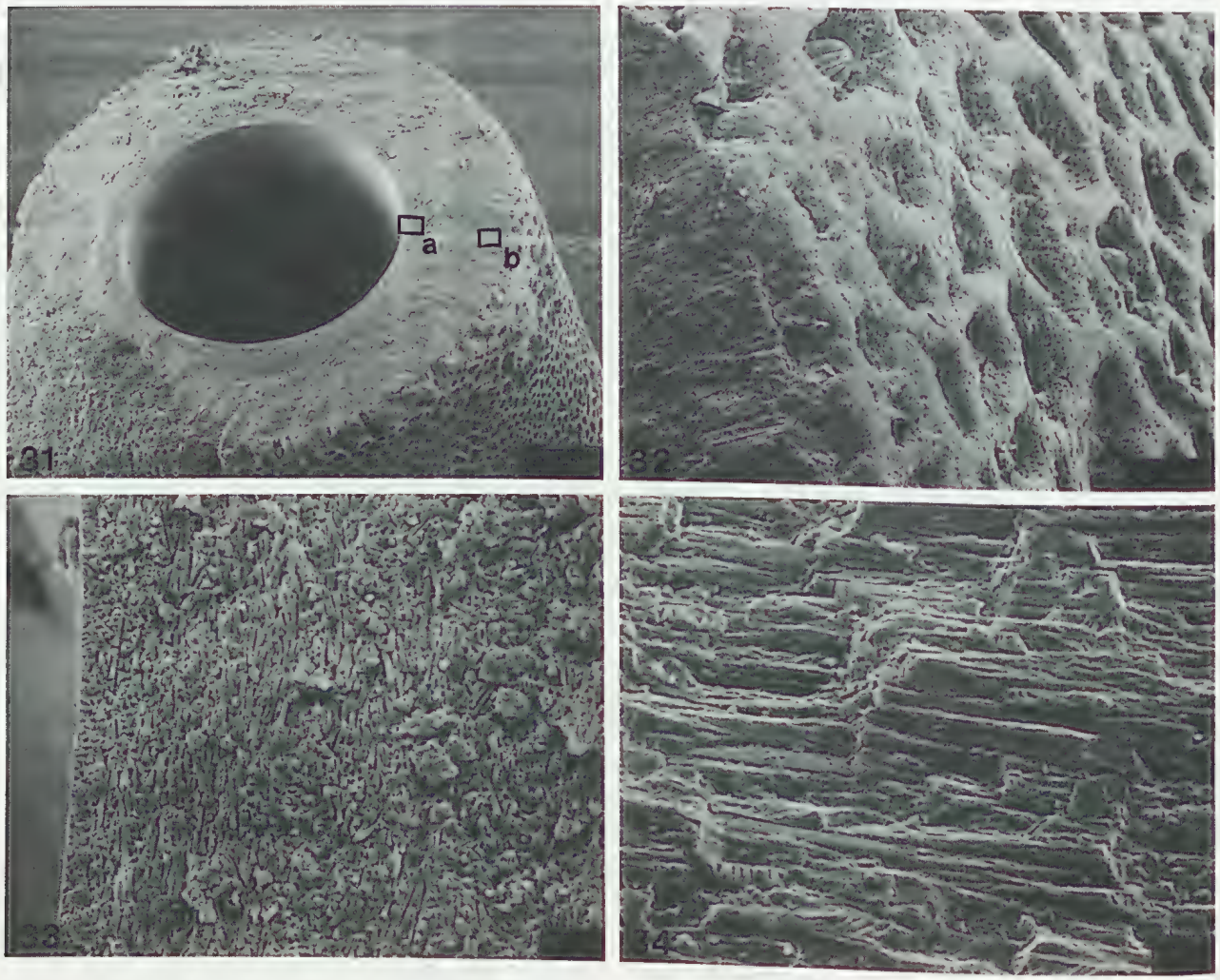
be variable anyway (compare for instance Figs 12 and 18), it is impossible to guess what length is missing. When the apex breaks off during life, the animal may block the increased posterior access to its tube by the formation of a tabula with 6 foramina (compare ten Hove, 1973:19; Bandel, 1986:68). We have observed this phenomenon only once, in a tube from off Oga (stn M).

Although there is a wide overlap in the tube measurements between different populations, the arcuation (arc, see below) and maximal width of the tube may give statistical differences. For instance, the following figures are derived from a series of at least ten tubes from four different locations:

| | Maximum tube width | Arcuation index |
|---|---|---|
| Tadjourah | 1.2-**1.63**-1.9 | 18.4-**25.4**-35.7 |
| | (SD = 0.28) | (SD = 5.9) |
| Shimoda | 1.1-**1.43**-1.7 | 11.9-**15.5**-21.7 |
| | (SD = 0.18) | (SD = 3.7) |
| Oga | 1.15-**1.30**-1.4 | 12.5-**16.0**-19.6 |
| | (SD = 0.08) | (SD = 2.0) |
| Reunion | 1.2-**1.55**-2.0 | 6.0-**11.9**-18.4 |
| | (SD = 0.05) | (SD = 3.5) |

The arc of the tube (height of inner curve/length $x$ 100) varies considerably (e.g. Fig. 5), from almost straight in a juvenile (6.0) to 35.7 in the most curved one (50 is the arc of a half circle). In a series of 14 rough and 10 smooth tubes, all entire (i.e. which started with an apex of about 0.16 mm) from Darnley Island (Figs 1,3), most had an arcuation index of about 17 and no statistical difference could be detected. Most samples had insufficient intact tubes for this kind of analysis, though the overall impression is that differences as given above are a result of geographic rather than bathymetric variation.

*Branchiae.* Up to 14 (generally 12) branchial radioles on each side, arranged pectinately, and not connected by a branchial membrane. The first left and first right normal radiole have about twice the diameter of the following ones. Pinnules increase in length distally, where they are about three to four times as long as the rhachis is wide;



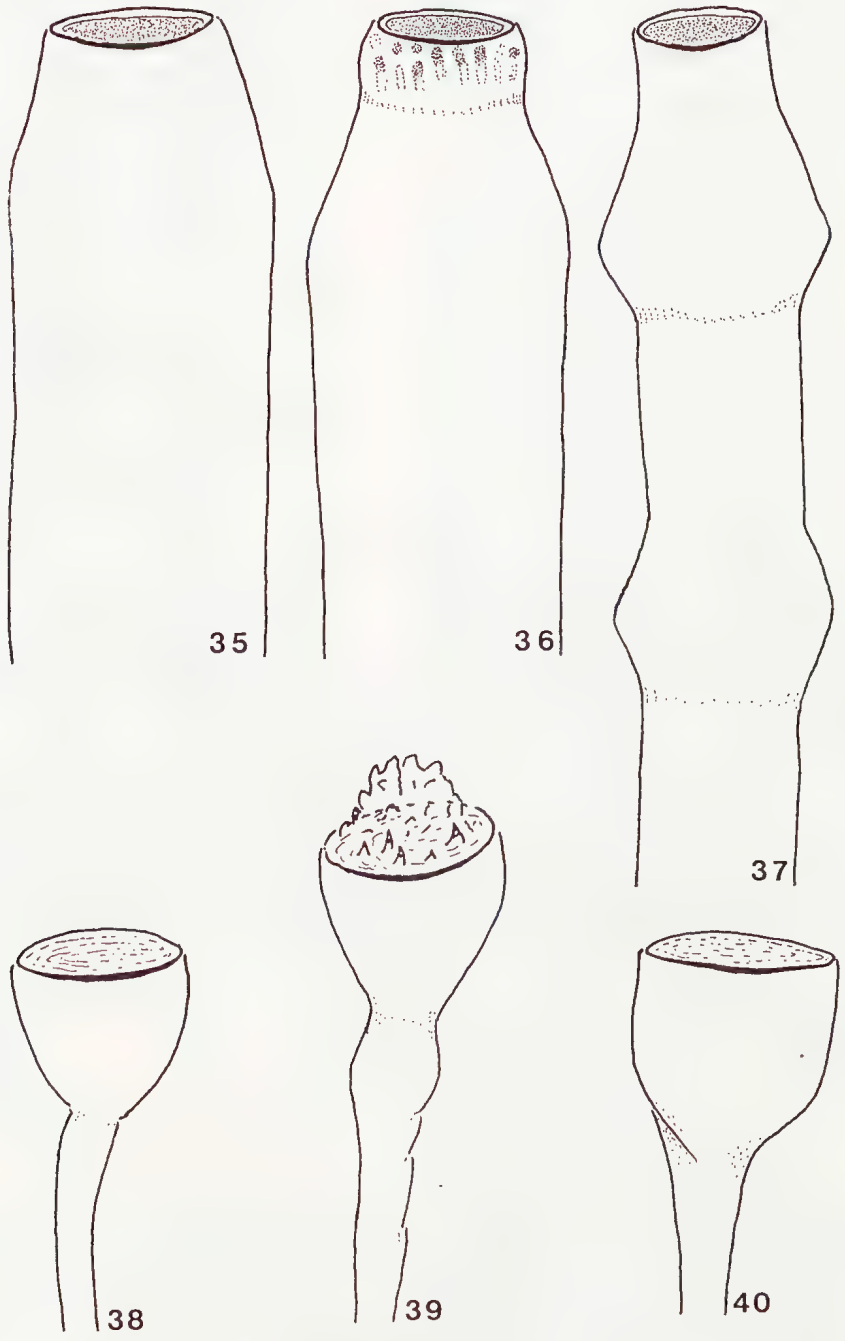

**Figs 31—34.** *Ditrupa gracillima.* Scanning electron micrographs of transversely fractured rough tube. Japan, off Kushimoto. 31: low magnification to show location of detail photographs: a = 33, b = 34; 32: detail of rough outer surface of tube, and of large prismatic crystals in outer part of wall; 33: high power magnification of inner criss-cross layer; 34: high power magnification of outer prismatic layer.

terminal filament not especially developed, but may be up to twice as thick as a normal pinnule. Branchial eyes and stylodes are absent.

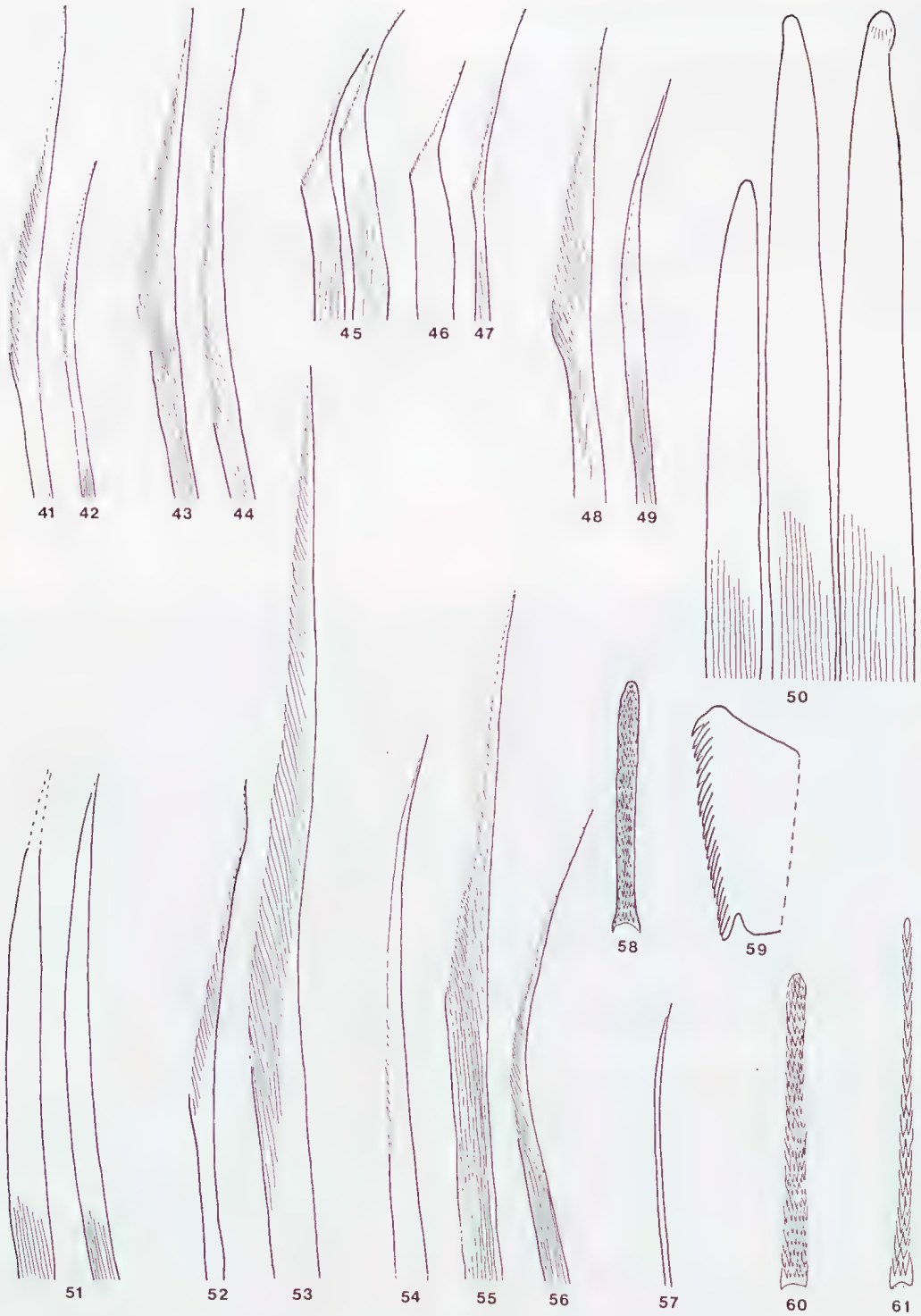
*Peduncle.* Smooth and circular in cross-section. Its insertion precedes the first radiole on the left side, but is displaced inward from the half circle of normal radioles. There is no pseudo-operculum. A lost operculum is regenerated from the rudiment of the peduncle. Distally, there is a smooth transition as the peduncle swells to become the opercular bulb (Fig. 40).

*Operculum.* Globular, with a distal chitinous endplate. The endplate is flat and circular, lacking both ornamentation (Fig. 38) and talon. The globular ampulla has the form of an inverted cone with convex walls. (In a small number of animals from north Queensland, these walls were slightly concave). The endplate is sometimes overgrown by athecate hydroids (Fig. 39). Diameter of operculum up to 1 mm, length of ampulla up to 1.2 mm; both varying according to population.

*Collar and thoracic membranes.* Generally the collar is high, with an entire edge. The margin sometimes looks serrated, if fixed when closely pressed against the radioles.




**Figs 35—40.** *Ditrupa gracillima* — 35: anterior tube part, common form, Townsville; 36: anterior tube part, thickened orifice with indentations, possibly caused by epibionths, La Réunion; 37: anterior tube part, monilifera-form, Indonesia; 38–39: opercula, Tadjourah, 39: operculum, covered by athecate hydroids; 40: operculum, Red Sea.




**Figs 41—61.** *Ditrupa gracillima* — 41–42: thoracic setae, first setiger, Tadjourah; 43–44: thoracic setae, fourth setiger, Tadjourah; 45: almost geniculate setae, first setiger, smooth tubed specimen, Palau Island; 47: almost capillary seta, first setiger, smooth tubed specimen, Palau Island; 48–49: fourth setiger, smooth tubed specimen, Palau Island; 46: Kushimoto, rough tubed specimen, almost geniculate seta, first setiger. 50–51: first setiger, acicular and capillary setae, Oga; 52–53: fourth setiger, Oga. *Ditrupa arietina* — 54: first setiger, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559); 55–56: fourth setiger, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559); 57: abdominal capillary, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559); 61: edge view of thoracic uncinus, setae and uncinus. South-west off Palma, Canary Islands (ZMA tH 559). Not to scale. *Ditrupa gracillima* — 58–59: uncini, first setiger, edge and side view, Oga; 60: thoracic uncinus, syntype, edge view. Not to scale.

The collar is continuous with the thoracic membranes, and without any lateral incisions. The thoracic membranes end just anterior to the first setiger.

*Thorax*. The thorax has only 6 setigers, all uncinigerous. Collar setae are absent. The first setiger occupies a place similar to that of the collar setiger in other serpulids and is widely spaced from the remaining 5 setigers. All thoracic setae are limbate and of 2 sizes (e.g. Figs 41–44). In the populations from south Japan and the Palau Islands, the first setiger has more or less geniculate setae as well (Figs 45–47). Worms from the Sea of Japan and Korean Straits show acicular setae (Fig. 50), as mentioned by Hong (1984, fig.4h). *Apomatus*-setae are absent. Uncini along the entire thorax are rasp-shaped, with about 30 rows of 3–5 curved teeth, the most anterior apparently bifurcate (Figs 58–60). A pair of prostomial eyes of up to eight pigmented spots is situated within the tissue at the base of the branchial lobes.

*Abdomen*. Up to 55 abdominal segments, though this number varies according to population (Tadjourah: 44–**48.4**–55, SD=3.8, n=10; Shimoda: (40)42–**46**–53, SD=4.1, n=5; Oga (30)32–**36.8**–40, SD=2.3, n=10). Uncini are rasp-shaped, with about 25 rows of 4–6 teeth (this number increases slightly towards the pygidium). All setae are capillary (Fig. 57). The pygidium is bilobed. There is no posterior glandular pad.

*Size*. Length up to 25 mm, generally about 16 mm. Width of thorax up to 1 mm. Branchiae and operculum account for one third to one fifth of the entire length.

*Colour*. Branchial radioles are transparent with red-brown pigment bands.

*Ecology*. i) Distribution with depth. Although present records indicate that tubes of *D. gracillima* have been collected to a depth of approximately 1,000 m, the bulk of living specimens occur only above 130 m. Of live material collected, only "monilifera" forms (i.e. with four to ten annular thickenings in the tube) have been observed from greater depths (75–650 m). Between one and three such annuli may occur in juvenile tubeparts of almost any shallow population. Often the annuli are positioned near the apex, though occasionally the first and only annulus occurs near the orifice. Moreover, the incidence of occurrence as well as the number of annuli apparently increases with depth (Fig. 62). In larger samples of the "monilifera" form it proved to be impossible to find an obvious ratio between size of tube and number of annuli. Annuli are irregularly spaced and variable in thickness. Exceptionally a tube may score four annuli when first measured, yet score six on a subsequent examination. In view of this, and since the material is scanty, the "monilifera" form is regarded as an ecophenotypic variation.

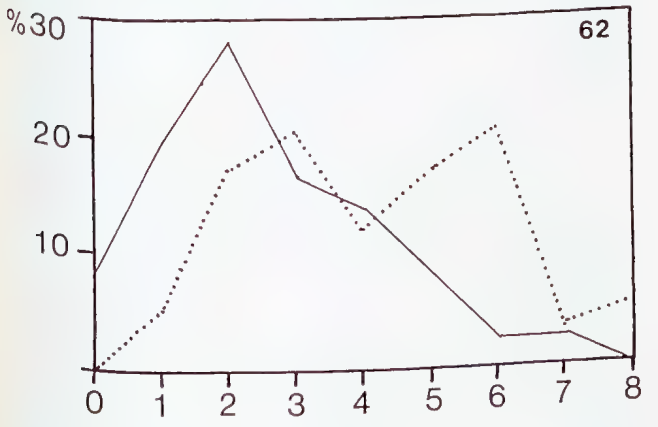



**Fig.62.** Monilifera-form, number of annuli (horizontal axis) in populations from different depth. Vertical axis: % of occurrence. Continuous line: La Réunion, 75-90 m (n = 36); dotted line: the Comores, 530-535 m (n = 59).

ii) Behaviour. Most authors agree that *Ditrupa* can move around. Sips (personal communication) mentions that when placed on top of the substrate, *D. arietina* can come out of its tube for the greater part of its length. Shifting its weight around, it can turn over its tube from lying on the right side to lying on its convex side or even its left side.

Some preliminary behavioural observations are available for "smooth" and "rough" specimens from Townsville. When placed in dishes with fine muddy sediment taken from their natural habitat, smooth tubed specimens use their branchial crown to burrow actively. Both whorls of radioles are flexed outwards proximally but held inwards distally and used as limbs for excavating a depression in the sediment. This is then used as an anchoring point from which the rest of the worm and tube is drawn forwards into the sediment by muscular flexion of the partially extended thorax. (At times during this process the entire thorax may extend from the tube). This procedure is repeated until the anterior portion of the tube reappears above the sediment at an angle of about 45° and the posterior apex is just exposed at the other end. The branchial crown is expanded into a small depression which it forms at the surface of the sediment when the tube re-emerges. This is likely to be the natural posture of this species in the environment. Worms thus positioned are able to continue filter feeding while remaining almost indiscernable against the sediment background.

This posture appears to conform more or less to Bandel's (1986:73) observations on *D. arietina*, but differs from Gambi's (1986:19) deductions. It is also in partial disagreement with Wilson's (1976:294) observations. From the relative abundance of tubes with solitary corals attached to the concave side, he supposed that the normal orientation of *D. arietina* is in a plane more or less vertical to the surface, with the convex side of the tube upwards, and the apex slightly buried. Given the angled posturing observed in the aquarium, however, it would be quite feasible for corals to settle on the anterior section of the tube and particularly on the concave side.

Also, the epibiotic relation between *D. arietina* and *Hydroides norvegica* Gunnerus, 1768, as figured by Gambi (1986), is unlikely to have developed in an orientation almost parallel to the surface. A similar epibiosis involving *H. multispinosa* Marenzeller, 1885 and *Spirobranchus latiscapus* (Marenzeller, 1885) was noticed in the material from the Sea of Japan, off Java respectively. Yet another, so far unidentified, epibiosis has been observed: in about 15 tubes, all with at least one "monilifera" annulus, there is a slightly raised brim around the orifice, ornamented with an irregular pattern of shallow indentations (Fig. 36). This has been observed in fossil

tubes as well.

Two interpretations are possible for these epibioses: in the environment the worms either orient their tubes at an angle above the sediment surface (enabling other organisms to use it as a safe anchoring place), or settled organisms prevent the worms to maintain the normal position, a hypothesis favoured by Wilson (1976).

Interestingly, we were unable to induce rough-tubed specimens to burrow in the aquarium, although they used the same technique as the smooth-tubed forms to manoeuvre over the sediment surface and flip the tube from side to side. When a more sandy sediment was provided, neither "rough" nor "smooth" specimens could be induced to burrow.

iii) feeding. Hong (1984:45) assumes that the genus may be a surface deposit feeder, and in a position more or less parallel to the surface, it would be possible for the worms to exploit this food source. However, filter-feeding was the only feeding strategy we observed in our aquarium specimens, even in those worms that lay flat on the sediment surface. Bandel (1968: 73) probably is correct in his observation that filter feeding is the main method to collect food.

**Nomenclature.** Despite the extensive synonymy, the oldest available name is *Ditrypa gracillima* Grube, 1878. Fortunately Grube's description is based not only on empty tubes but on specimens as well. Hence, by elimination we propose the specific designation *gracillima* for this Indo-Pacific *Ditrupa*.

The name *laeve* or *laevis* has a confused and confusing history. *Dentalium laeve* Turton (1819:256) was proposed as a new name for the preoccupied *Dentalium politum* (*non* Linnaeus, 1767) Turton (1819:38–39, Torbay, U.K.), both of which are most likely scaphopods judging from the descriptions.

*Dentalites laeve* Schlotheim (1820:93–94) is a primary junior homonym of *Dentalium laeve* Turton. Figured by Chenu (1842–1855, livr.7, pl.7 fig.8a,b), it appears to be a fairly large serpulid or scaphopod.

*Dentalium laeve* (*non* Turton, *nec* Schlotheim) Brazier, 1877 (Figs 1,3) is a junior primary homonym of *Dentalium laeve* Turton. It must, therefore, be permanently rejected (International Code of Zoological Nomenclature, article 57b) as suggested by the first reviser Bretnall (1921: 155–156). However, the new name proposed by Bretnall, *Ditrupa brazieri*, is a junior synonym of *Ditrupa gracillima*. According to Bretnall (1921:155), Hilgard & Hopkins (1878) also used the name *Dentalium laeve* for a fossil from the USA.

*Serpula laeve* Montagu (1803:524), also mentioned by Pennant (1812:364) and Turton (1819:157) belongs to the Foraminifera. The fossil *Serpula laevis* Goldfuss (1826–1833:236; 1834–1840:pl.70 fig.3) and *S. laevis*: Geinitz (1873:285, pl.63 figs 13–14) have triangular adnascent tubes, and were referred to two different species of *Parsimonia* by Regenhardt (1961:38) and Lommerzheim (1979:140).

The next oldest name for Indo-Pacific material appears to be *Dentalium strangulatum* Deshayes (1825:372–373, pl.16 fig.28), referred to *Ditrupa* by Mörch (1863:426). However, this is also very confused. A syntype of *Dentalium strangulatum* (Fig. 21; MNHN, Paris) is labelled "Voyage aux terres australes, Péron et Les. 1803", and also bears a crossed out label "Dentalium cornée". It is the specimen figured by Deshayes (1825: pl.16 fig.28). However, neither label nor Deshayes' text give a proper locality, both simply state that the specimen was brought back by the expedition. Vain attempts have been made to find reference to *Dentalium* in Péron's voluminous reports (1807, 1816). The expedition under captain Baudin left Australia in 1803, returning to Europe via Africa. According to Lamarck (1818:345) *Dentalium corneum* "Habite les mers d'Afrique", and his material (MNHN, Paris) is labelled "Péron et Leseur, Expédition du Cap. Baudin, 1803". It may be inferred from this that Lamarck's material, at least, was collected in Africa. His fragmentary tubes, with a width of 2.1–3.0 mm and faint arcuation, definitely belong to the Atlantic species *Ditrupa arietina*. The syntype of *Dentalium strangulatum* has a width of 2.2 mm, but the fragment is only 14.5 mm long. Deshayes mentions a length of 30 mm. Except for a slight difference in colour, it would fit nicely in the series of Lamarck's *Dentalium corneum*. In all of the hundreds of Indo-Pacific tubes now studied, only two tubes are over 2.1 mm in width and 30 mm in length. Conversely, these dimensions are quite normal for *Ditrupa arietina*. On its outward voyage, the expedition spent some weeks collecting around the island of Tenerife after dropping anchor in Santa Cruz (Canary Islands). *Ditrupa arietina* can be found here by the thousand (ten Hove, unpublished). In view of this, it is far more likely that the syntype was collected in the Atlantic, than in the Indo-Pacific.

It would appear that Deshayes mainly referred to fossil material from Europe in his description of *Dentalium strangulatum*. He included *Dentalium incrassatum* Sowerby (1815:180, pl.79 figs 3–4; figured by Chenu, 1842–1855,Livr.7, pl.7 fig.19) from the U.K. Eocene, and *Dentalium coarctatum* Brocchi (1814:264, pl.1 fig.4; mentioned in Pilsbry & Sharp, 1898:242) from the Italian Pliocene. Consequently *Ditrupa strangulata* has been used more often for European fossils (e.g. Wrigley, 1951:191). More recently, Zibrowius & ten Hove (1987:fig.3; Fig.25 herein) have shown that these fossil tubes are extremely similar to those of the Recent *Ditrupa arietina* O.F. Müller, 1776 at an ultrastructural level. Fossil Italian Plio-Pleistocene material in the AM (Figs 22,24; W 201219, 201238, 201302) confirms this opinion, these tubes can hardly be distinguished from Recent material of *Ditrupa arietina*. Other Recent material included in *Dentalium strangulatum* by Deshayes is *Dentalium corneum* as described by Lamarck (1818:345) from Africa (though not the material of Linnaeus, 1767:1263 which, if Deshayes may be believed, is an insect larva). Unfortunately, no original material of Linnaeus could be found in the collections of the Linnean Society, London nor in Uppsala. As stated above, *Dentalium corneum*: Lamarck is synonymous with *Ditrupa arietina*. To complicate matters, *Ditrupa cornea* (L.) has been used for Eocene Hungarian material by Bohnné Havas (1981) in her study of the ultrastructure of the tube wall. The material figured as *Dentalium strangulatum* var. by Chenu (1842–1855, Livr.7, pl.6 figs 24, 24a,b) looks similar

to the rough tubes (24), smooth tubes (24b) and "monilifera" forms (24a) described herein. Without access to all the actual material, it is not possible to evaluate the full implications of Deshayes' taxon and it evidently is a mix of several forms and a *nomen dubium*.

**Distribution.** Mostly tropical: Indo-west Pacific.

## Remarks

The description of *Bonhourella insignis* Gravier, 1905 (and 1906–1908, figs 301–302), particularly the unique arrangement of the first thoracic setiger in relation to the remaining ones, point to a synonymy with *Ditrupa*, the more so since Gravier mentions *D. arietina* from the same station. The latter material has been studied and belongs to *D. gracillima*. The holotype (MNHN) was examined by Zibrowius in 1971, and he confirms this suspicion (*in litteris*).

With regard to *Ditrupa australis*, as figured by Dew (1959, fig.18A), the original description indeed points to a [juvenile] specimen of *Ditrupa*: "The walls of the posterior [Bretnall errs here, he refers to anterior] opening are thickened and slightly contracting in perfect specimens". However, both Bretnall and Dew's figures appear to be of either damaged tubes or a scaphopod.

The figure of *Ditrupa amphora* Dew (1959:48, fig.18D), with a distinct "shoulder" anteriorly, is extremely similar to some juvenile tubeparts for example in the type series of *Dentalium laeve* Brazier. Some of those juvenile parts even show three more or less annular "shoulders", just like the ones in the form described as var. *monilifera* by Fauvel (1932:fig.12), before giving way to the normal bright white and gradually broadening tube of an adult worm.

The tube surface was researched in some detail to determine the nature of those with a rough appearance. It has not been possible to show an epibiotic origin. Colleagues familiar with calcareous algae, bryozoans and sponges could not recognise the structure. Examined optically in a geological thin section, there is no clear boundary between the central transparent and the outer rough layer. There is room for doubt, though, as scanning electron micrographs suggest a discontinuity in this region. However, the mineralogy of the inner opaque and outer rough layer is the same. Both are purely calcitic, as checked both optically and by x-ray diffraction. Some tubes start smooth, and halfway their lengths switch gradually to rough or vice-versa. A couple of specimens even start with a rough tube part, change to smooth, and back again to rough around the orifice. Smooth and rough tubes co-exist in many localities over the entire distribution of the species. We are of the opinion that the rough surface, rather than caused by some unknown epibiont, is a property of the animal. The 1:3 occurrence of rough:smooth tubes points to a Mendelian heredity, perhaps influenced by environment. On first sight, rough tubes are more massive in proportion than the smooth ones. Up to a length of 19 mm, rough tubes are 10 to 35% wider than smooth tubes. However, the effect is lost in tubes over 20 mm. We have not been able to find other differences between rough and smooth tubes in an extensively measured series of 40 from Darnley Island, except that smooth tubes reach a larger size (30.4 mm, width 2.0 mm against 22.4 mm, 1.7 mm) in this sample.

A similar rough surface structure is mentioned for the fossil *Sclerostyla polyforata* Jäger (1983:87–88, pl.10 figs 10–12), and for *Dentalium entalis* as figured by Chenu (1842, Livr.7, pl.3 fig.2). We also found it in tubes of *Protula* specimens from Java (8°26'S, 114°29'E, stn 6, coll. Th. Mortensen, 5 Apr. 1929, 70 m; ZMK).

Although Cheng is mistaken in his remark that the inner layer of the tube is of organic material (it is calcareous as well, cf. Bohnné Havas, 1981:pl.6; Zibrowius & ten Hove, 1987:fig.3), the chevron structures mentioned by him are indeed visible in thin sections. By comparing these with the orientation of the crystals in the outer transparent layer of the tube (these face diagonally outward and slightly forward), it is indeed possible to infer the posterior apex of the tube in paleontological material.

It is remarkable that the first setiger (apparently second segment) has taken over place and function of the collar setae of other serpulids. Limbate setae are the plesiomorphic character-state, since they occur in other thoracic segments too and are the most common type in all serpulids. Two populations (Sea of Japan and Korean Straits on the one hand, south Japan and Palau Island on the other) are characterised by a unique apomorphy: special setae in the first setiger. All other material (*D. arietina* from Marseille and Madeira, syntypes of *D. gracillima*, rough and smooth tubed specimens from La Réunion, Madagascar, Comores, Red Sea, South Arabia, Townsville and the "monilifera" form from south Japan) has limbate setae only. However, we were unable to find a consistent difference in any of the other characters checked. For instance, although tubes from the Sea of Japan are invariably smooth, while those from south Japan are rough and/or smooth, the measurements for these populations are more similar to each other than to the population from Tadjourah. On the other hand there is an almost complete overlap in number of abdominal setigers beteen Tadjourah and south Japan, while the mean and maximum are considerably lower in the Sea of Japan. We therefore decided not to attribute a specific rank upon this single apomorphy. In view of the chorology of the forms with aberrant first setigers, it is possible that speciation is about to occur.

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# Two New Species of the Previously Monotypic Congrid Eel Genera *Poeciloconger* and *Macrocephenchelys* from Eastern Australia

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ABSTRACT. *Poeciloconger kapala* n.sp. (Congridae, Bathymyrinae), described from a single 540 mm SL specimen trawled in about 50 m north of Sydney, differs from the only other species of the genus, *P. fasciatus* Günther, 1871 (tropical Indo-Pacific), in having tan body colouration and small ovoid light spots anteriorly rather than dark spots and irregular bars on a light background, generally molariform rather than sharp vomerine teeth, and fewer vertebrae (148 rather than 154–158). *Macrocephenchelys soela* n.sp. (Congridae, Congrinae), described from five specimens 259 to 298 mm SL trawled in 350 m off the north-east Queensland coast, is distinct from the unique *M. brachialis* Fowler, 1934 (Philippines, Mozambique Channel) in having a more robust rather than slender body, a more anterior dorsal origin, a larger branchial aperture, a longer snout, molariform vomerine teeth, and fewer vertebrae (150–151 rather than 179–182).

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Some 160 genera of eels (Anguilliformes) are currently recognised. Of these about one-third are monotypic, though this possibly reflects imperfect knowledge of the genera concerned on a worldwide basis rather than excessive generic splitting within the Anguilliformes generally. Monotypic genera are more a feature of the Ophichthidae (i.e. 18 out of 55) and Chlopsidae (four out of seven) though these families include many small, cryptic, fossorial forms and for that reason are almost certainly incompletely known. Judging by the diversity of their larvae, which are more accessible to collecting, further genera and species can be expected to be described in these families. The Synaphobranchidae and Congridae include rather many monotypic genera which could be explained by incomplete collecting of these generally deep water eels in many parts of the world.

This paper reports a second species of *Poeciloconger* Günther, 1871 and of *Macrocephenchelys* Fowler, 1934, two hitherto monotypic genera of Congridae. Both new species were collected on the Australian east coast, the former in shallow, inshore water north of Sydney, the latter in deeper water further to the north, off Townsville.

*Poeciloconger* was originally reported from an

approximately 300 mm TL specimen of *P. fasciatus* Günther, 1871 from Sulawesi (Celebes), and again by Günther (1910) from an approximately 508 mm TL specimen from Tahiti. Günther did not state why he considered the genus to be distinct from other congrids, though he must have noted the rather stiff caudal tip and reduced caudal fin, as well as the conspicuous spotted to banded body colouration. However, the caudal tip in species of other congrid genera (*Ariosoma* Swainson, 1839 and *Gnathophis* Kaup, 1860) as well as variously in the so-called 'garden eels' of the congrid subfamily Heterocongrinae, is also abbreviated and somewhat stiffened. Furthermore, while most congrid species have rather nondescript body colouration, several species of Heterocongrinae are distinctively marked. Though not as obviously coloured as *P. fasciatus*, the congrid eel described here is also distinctive in this family in having a body colouration of profuse, small, ovoid, light-coloured spots on a dark background. It has the terminal few centimetres of the caudal region firm rather than flexible, and an abbreviated caudal fin. In these characters it generally agrees with *P. fasciatus*. More profoundly, it agrees in having unsegmented dorsal and anal fin rays (as readily determined microscopically or from a radiograph), a feature which distinguishes the subfamily Bathymyrinae from the Congrinae, in which the fin rays are segmented. The osteology of *Poeciloconger* has not yet been studied but the character of the fin rays indicates that it should be aligned with the Bathymyrinae rather than with the Congrinae as Smith (1984) implies. The maxillary bands of teeth meet anteriorly in the midline, thus enclosing the premaxillary-ethmovomerine band wholly within the mouth. In effect, this band does not freely project as it does in many of the approximately 30 genera of Congridae, though to a varying degree. A disagreement between the new species and *P. fasciatus* is that in the latter the premaxillary-ethmovomerine teeth are relatively sharp and slightly recurved ("villiform" in Günther's terminology) while those of the new species, for the most part, are low, rounded and molariform. They are thus rather similar to those of *Ariosoma* (Bathymyrinae) and *Gnathophis* (Congrinae). The nature of the teeth on the roof of the mouth ("vomer") is often, though not always, a useful discriminatory character of most genera of congrids. Despite this difference in dentition, the overall similarities between the new species and *P. fasciatus* are considerable, but insufficient in my opinion to justify separation of the new species at the generic level.

*Macrocephenchelys* is known only from *M. brachialis* Fowler, 1934, originally reported from two specimens collected in 670 m from the Macassar Strait, Indonesia by the *Albatross* in 1909. Because its snout and cephalic morphology is so unusual, the genus and species has had a chequered history amongst the eel families though it has for some time now been regarded as the single representative of the congroid family Macrocephenchelyidae. McCosker, Böhlke & Böhlke (1989) recently referred this family to the Congridae and Smith (1989) discussed the relationship of *Macrocephenchelys* itself to members of the subfamily Congrinae, to which the genus was more specifically referred. There would seem to be good reasons for accepting these views. Robins & Robins (1971) reviewed the osteology and relationships of *M. brachialis* while Karrer (1982) reported a third specimen from the Mozambique Channel (exact locality in doubt since there were two labels with the specimen indicating either south-western Madagascar in 550 to 555 m or further north in 1200 m). The five specimens reported here from off Townsville in 345 to 350 m readily agree with *Macrocephenchelys* in having a distinctively short, bulbous snout with swollen, protruding plicae (folds) overhanging the mouth and a long, narrow, pectoral fin directed obliquely upwards. Though somewhat reminiscent of *Simenchelys* Gill (Synaphobranchidae, Simenchelyinae) and the ilyophin synaphobranchids in the character of the snout, *Macrocephenchelys* is highly distinctive and cannot readily be mistaken for any other genus of eels. In having a much more robust form, the dorsal origin over the middle of the pectoral (i.e. much further forward than in *M. brachialis*), fewer pores before anus (29–30 compared with 33–34), a shorter tail, and fewer vertebrae (i.e. 150–151 compared with 179–182), the new species is readily distinguished from *M. brachialis* and is described here as new.

## Materials and Methods

Institutional abbreviations are as given in Leviton *et al.* (1985). Measurements were made with dial calipers. Total lengths are used throughout since the caudal fin length is insignificant as a proportion of TL; preanal length is straight line distance between tip of snout and middle of anus; predorsal is snout tip to base of first dorsal ray; head is from snout tip to uppermost extremity of branchial aperture; snout is from snout tip to anterior margin of fleshy orbit; eye is greatest (horizontal) diameter of orbit; interorbital is least distance between dorsal margins of orbits; mouth is from snout tip to extremity of exposed maxilla where it becomes covered by integument; branchial aperture is distance between upper and lower extremities; pectoral is measured from middle of base to its tip; depth is greatest depth of body, usually at pectoral base. Pectoral rays are counted on right side after integument has been turned back from base to expose the rays; preanal pores are counted to a vertical from anus; total vertebrae exclude urostyle as a separate element. Cephalic pores include those from tip of snout before and above anterior nostril to above eye (supraorbital canal, though the most anterior pore of this series should strictly be termed an ethmoid pore), from behind anterior nostril along edge of upper jaw (infraorbital canal), behind eye (postorbital canal, though this is strictly part of the infraorbital series), along lower jaw onto preopercular region (preoperculo-mandibular canal) and occipital region (supratemporal canal, inclusive of a median dorsal pore). Radiographs were made with a soft X-ray machine and developed normally.

### *Poeciloconger kapala* n.sp.

Figs 1A–C, 2, Table 1

**Material examined.** HOLOTYPE: AMS I.25923-005, 540 mm SL, maturing female, collected by the New South Wales Fisheries Research Vessel *Kapala*, 11 Apr. 1985, 32°41'S 152°16'E to 32°44'S 152°15'E (off Port Stephens, New South Wales, Australia), capture depth 46–64 m, bottom trawl.

**Comparative material.** *Poeciloconger fasciatus* (5 specimens): holotype BMNH 1871.7.20.63 (305 mm TL),

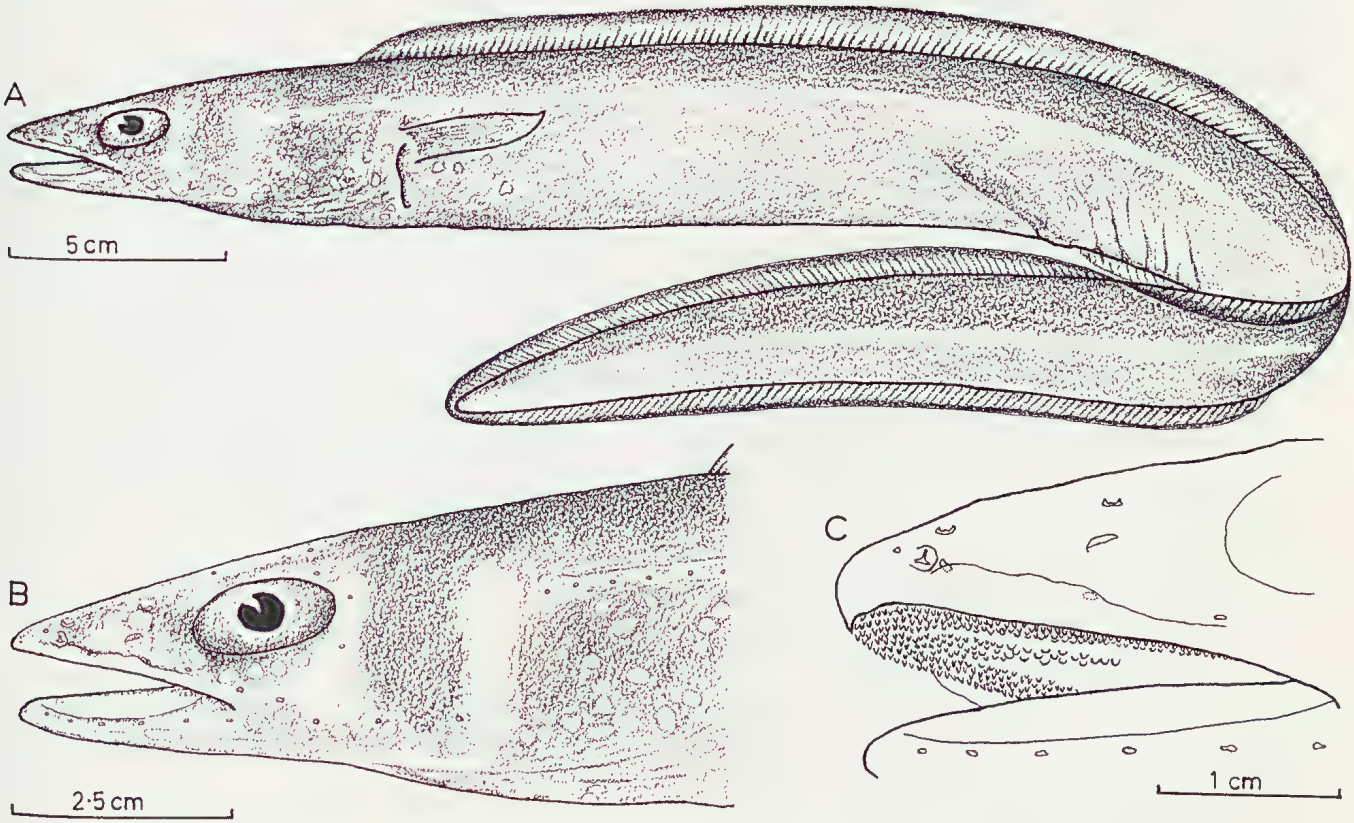


**Fig.1.** *Poeciloconger kapala*, holotype, 540 mm SL, AMS I. 25923-005. A: lateral view to show overall body form and colouration; B: lateral view of head detail; C: ventrolateral view to show maxillary and premaxillary-ethmovomerine teeth.

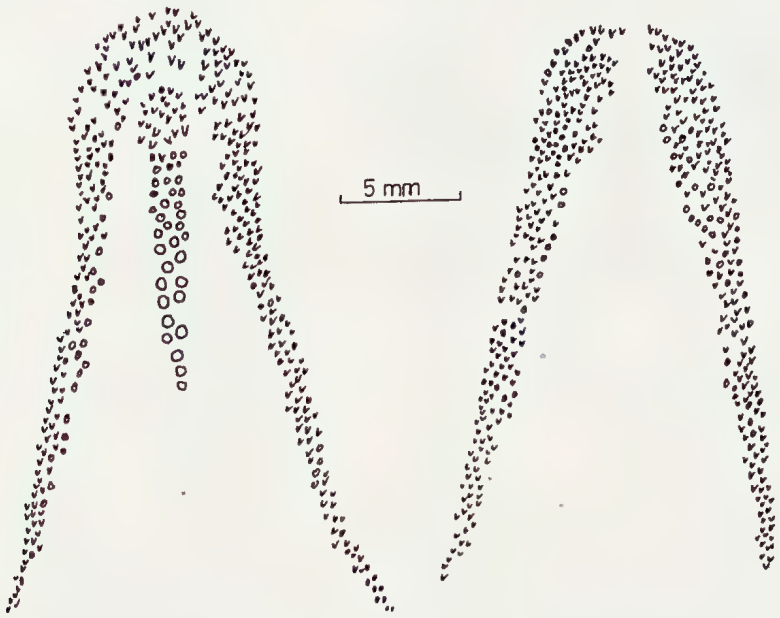


**Fig.2.** *Poeciloconger kapala*, holotype, 540 mm SL, AMS I. 25923-005: pattern of upper (left) and lower (right).

BPBM 29210 (140 mm TL), BPBM 29233 (217 mm TL), ANSP 135440 (581 mm TL), SMF 10931 (414 mm TL, radiograph only).

**Diagnosis.** Mid-greyish brown background body colour, covered with small, discrete, ovoid light spots, particularly over head, trunk and dorsal and pectoral fins; precaudal vertebrae 74; total vertebrae 147. Other distinctive characters include preanal 2.2 in TL, eye 5.1 in head, vomerine teeth on posterior half of bone molariform.

**Description.** Morphometric and meristic characters of the new species and *P. fasciatus* are given in Table 1. Other descriptive details of the holotype are as follows: body moderately elongate, caudal region firm, not delicate, and tapering to the caudal tip noticeably along posterior quarter of body length; snout relatively sharp (though probably more fleshy in life); lower jaw subequal to snout; anterior nostril weakly tubular, placed well back from snout tip, its rim complete; posterior nostril an inconspicuous narrow aperture well before and below horizontal diameter of eye, its upper margin free, the lower incorporated into snout; mouth cleft reaching to below anterior margin of pupil; well-developed upper and lower lips present; eye relatively large, oval; interorbital broad; branchial aperture vertical, large, extending from middle of pectoral base nearly to meet ventral profile; pectoral rather long and narrow, rounded posteriorly; dorsal origin somewhat before level of pectoral base and branchial aperture; preanal length almost half of total; dorsal fin equal in height along its length and about one quarter of body depth; anal fin similar but lower; caudal fin present but with very short rays and supported by a very firm, narrow, caudal tip; lateral line pores minute but relatively conspicuous, fewer than vertebrae, present to within 21 mm of caudal tip; cephalic pores present but inconspicuous, as follows: in supraorbital canal 1 small pore anterodorsal to anterior nostril followed by 2 larger pores, each with a flap-like rim, and then 2 small pores above orbit; in infraorbital canal 5 pores, the first immediately behind anterior nostril and partly hidden by front of upper lip, second pore hidden by lip, fourth and fifth below eye; in postorbital series 3 small pores; in preoperculo-mandibular series 9 pores; in supratemporal series 2 pores and a median dorsal pore.

Teeth on maxillary and dentary generally in 4–5 longitudinal rows, though reducing to 2-3 rows posteriorly (Figs 1C, 2); teeth in outermost rows conical, relatively

Table 1. Comparison of *Poeciloconger kapala* and *P. fasciatus*

| | P. kapala | P. fasciatus | |
|---|---|---|---|
| | AMS I.25923-005 Holotype | BPBM 29210 | BPBM 29233 |
| TL (mm) | 543 | 140 | 217 |
| SL (mm) | 540 | 138 | 216 |
| Preanal (% total) | 45.5 | 40.7 | 42.9 |
| Predorsal (% total) | 14.5 | 13.9 | 14.2 |
| Head (% total) | 17.0 | 16.8 | 17.9 |
| Snout (% head) | 21.6 | 22.1 | 23.2 |
| Eye (% head) | 19.4 | 15.3 | 15.3 |
| Interorbital (% head) | 13.2 | 8.5 | 13.5 |
| Mouth (% head) | 29.1 | 31.1 | 31.4 |
| Branchial aperture (% head) | 17.1 | 9.4 | 14.5 |
| Pectoral (% head) | 33.6 | 29.4 | 29.3 |
| Depth (% head) | 43.6 | 26.0 | 30.1 |
| Pectoral rays | 14 | – | – |
| Dorsal rays before anus | 68 | 64 | 81 |
| Dorsal rays (total) | 204 | – | about 246 |
| Anal rays (total) | 152 | – | about 180 |
| Predorsal 1.1. pores | 4 | 4 | 4 |
| Preanal 1.1. pores | 52 | 54 | 53 |
| Total 1.1. pores | 139 | 149 | – |
| Precaudal vertebrae | 74 | 85 | 80 |
| Total vertebrae | 147 | 158 | 154 |
| Cephalic pores: | | | |
| Supraorbital | 5 | 5 | 5 |
| Infraorbital | 5 | 5 | 5 |
| Postorbital | 3 | 3 | 3 |
| Preoperc.-mandibular | 9 | 10* | 10* |
| Supratemporal | 1+1 | 2+1 | 2+1 |

* several smaller pores are present in these small specimens.

sharp, especially anteriorly, in inner row some teeth low, rounded and molariform; teeth on premaxillary-ethmovomer in 4–5 rows anteriorly, tapering to 1–2 rows posteriorly, teeth subconical anteriorly but mostly (i.e. for posterior two-thirds) low, rounded and molariform on remainder of roof of mouth; maxillary bands meeting in front of premaxillary-ethmovomerine patch so that the latter does not project.

**Colour of holotype.** In alcohol, generally mid-greyish brown on head and above lateral line, lighter below and behind pectoral fin; on head the darker ground colour broken by 2 lighter bands immediately behind eye and at midpostorbital; on head, trunk, dorsal fin and pectoral fin scattered, small (average 3 mm), largely discrete, ovoid, light spots, more numerous on branchial region; a few similar spots on anal fin; dorsal and anal fins with broad, dusky outer portions for the whole of their lengths, the actual margins black. Colour when fresh similar to above, but pectoral fin grey black, dorsal fin with more obvious light spots, body above lateral line rather dark with positions of myosepta lighter so that the muscle segmentation above lateral line is very obvious.

Holotype a maturing female, heavily packed with ova, each about 0.7 mm diameter. Condition of holotype: generally rather dehydrated; a ventral incision in body wall made to determine sex of specimen.

**Remarks.** This species is named for the New South Wales State Fisheries research vessel *Kapala* from which the holotype was collected and which has added substantially to collections of fishes from the east coast of Australia over recent years. The species name is to be considered a noun in apposition.

The holotype was collected by bottom trawl in relatively shallow water off the New South Wales coast north of Sydney. The bottom there is described verbally as "...trawlable..." (K. Graham, N.S.W. State Fisheries) and is very likely to be sand as it is offshore of extensive dune beaches. There is, however, no precise information available on the area of capture. *Poeciloconger fasciatus* was reported by Klausewitz (1971) from a single 414 mm TL specimen (SMF 10931) buried tail first in the sandy bottom off Nosy Iranja, Madagascar in 15 m. Randall (1986) recorded this species from a 217 mm TL specimen (BPBM 29233) in sand at Enewetak lagoon, Marshall Islands in 2.5 m and a small specimen (BPBM 29210) from sand off Kailua, Hawaiian Islands in 32 m. During February, 1989 Randall and colleagues observed and photographed on several occasions a large *P. fasciatus* on about 20 m at Molokini, Maui, Hawaiian Islands. When first observed the specimen was lying more or less vertically in a hole in the sandy bottom, the diameter of the hole being larger than that of the eel. Only a small portion of the head projected from the entrance to the hole. The eel was induced to leave the hole and swam freely and quietly in front of the observers where it was photographed. The species also occurs at Tahiti (Günther, 1910) and at Mauritius (ANSP 135440, 581 mm TL, Flic-en-Flac, west coast, collected by D. Pelecier, 1973). The two *Poeciloconger* species clearly live in rather similar conditions, and as judged from the caudal structure of *P. kapala*, i.e. a stiff caudal tip and reduced caudal fin, it is likely that the Australian species exhibits similar "...tail first..." burrowing behaviour to that of *P. fasciatus*. Similar behaviour is known to occur for the congrids *Ariosoma anago* (Asano, 1962) and *Gnathophis habenatus* (Castle, 1963), the garden eels (Congridae, Heterocongrinae – numerous records) and certainly many Ophichthidae, in which the caudal structures are moderately to greatly reduced or even absent, being replaced in nearly all Ophichthinae by a hard, finless caudal tip. *Poeciloconger kapala* is warm temperate in distribution, while *P. fasciatus* is clearly tropical (Sulawesi, Tahiti, Madagascar, Mauritius, Marshall Islands, Hawaiian Islands). However, because these eels are fossorial and seemingly rare, further detailed information on their distribution may not be forthcoming for some time.

*Poeciloconger kapala* differs markedly from the only other species of the genus, *P. fasciatus*, in colour pattern and less obviously in vertebral number, shape of vomerine teeth and in several body proportions. *Poeciloconger fasciatus* is conspicuously marked with small to moderate sized, closely packed darkish brown spots on the head and postorbital, merging on the body to form partial to complete but dorsally divided vertical bars, these dark markings on head and body on a cream to pale yellow body ground colour. The juvenile 141 mm TL specimen from Hawaii is almost completely marked by wide, simple, vertical dark brown bars. The difference in total vertebral numbers (148 in *P. kapala*, 154–158 in four specimens of *P. fasciatus*) is not great but is comparable to differences recorded between species in other congrid genera, the number in *P. fasciatus* being consistently higher. Further specimens of *P. kapala* are required to establish the fuller extent of this disparity. *Poeciloconger kapala* also has molariform teeth on the posterior half of the vomerine portion of the premaxillary-ethmovomer (Figs 1C, 2) while those of *P. fasciatus* are notably sharper (Fig. 2, Klausewitz, 1971), confirmed also in the holotype, in the larger of the two BPBM specimens from the Marshall Islands and in the ANSP specimen from Mauritius. The preanal length appears to be somewhat greater in *P. kapala* (2.2 in total) than in *P. fasciatus* (2.4 in total), the head is shorter (5.9 versus 5.7–5.8 in total) and the eye larger (5.1 versus 5.9 in head).

### *Macrocephenchelys soela* n.sp.

Figs 3A–C, 4

**Material examined.** HOLOTYPE: CSIRO H1668-07, 288 mm SL, maturing male, CSIRO Fisheries Research Vessel *Soela*, Station SO6/85/04, 17 Nov. 1985, 22°35'3"S 153°46'7"E to 22°36'3"S 153°50'1"E (south of Saumarez Reef, Saumarez Plateau area, Queensland, Australia), capture depth 345–350 m, scampi demersal net trawl, 0220 hrs, CSIRO radiograph 432D. PARATYPES: CSIRO

H1668-04 (259 mm SL, female), same data as holotype, CSIRO radiograph 432A; H1668-05 (298 mm SL, male) same data as holotype, CSIRO radiograph 432B; USNM 307832 (298 mm SL, female), same data as holotype, formerly CSIRO H1668-06, CSIRO radiograph 432C; AMS I.29995-001 (271 mm SL, female) same data as holotype, formerly CSIRO H1668-05, CSIRO radiograph 432E.

**Comparative material.** *Macrocephenchelys brachialis* (1 specimen): holotype USNM 92347 (492 mm TL).

**Diagnosis.** Body rather robust, depth at anus 19% preanal length, dorsal origin over middle of pectoral, branchial aperture large and in front of pectoral base, rather simple snout plicae (folds), numerous, molariform vomerine teeth; 150–151 vertebrae and lateral line pores before anus 28–30; numerous, minute, sensory structures scattered over ventrolateral and ventral surface of trunk.

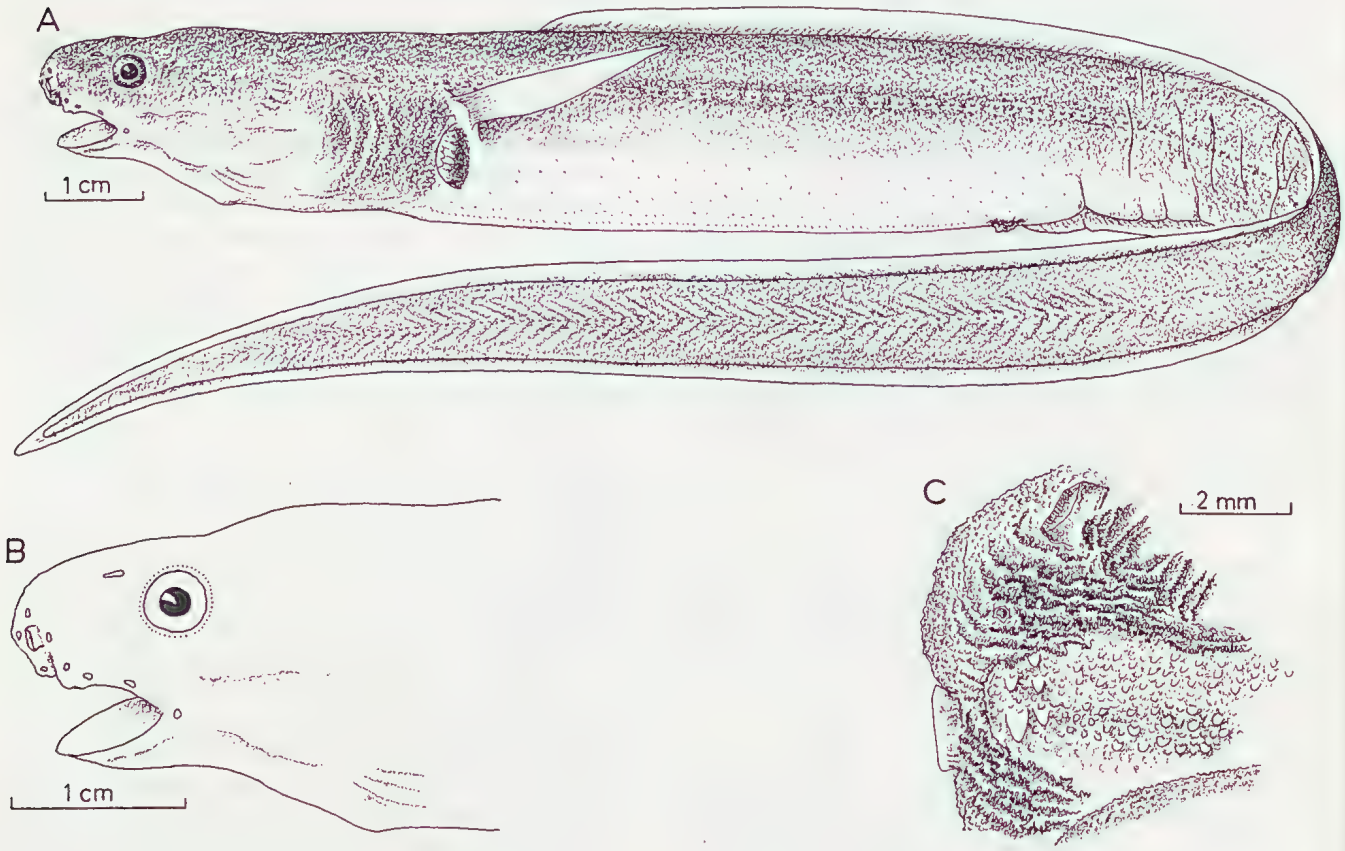


**Fig.3.** *Macrocephenchelys soela*, holotype, 288 mm SL, CSIRO H1668-07. A: lateral view to show overall body form and ventrolateral papillae on trunk; B: lateral view of head detail; C: ventrolateral view to show maxillary and premaxillary-ethmovomerine teeth and snout plicae.

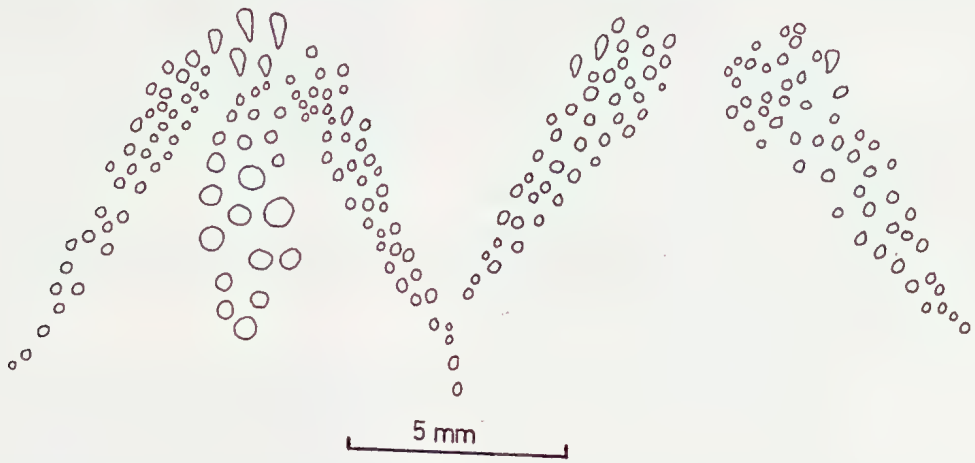


**Fig.4.** *Macrocephenchelys soela*, holotype, 288 mm SL, CSIRO H1668-07: pattern of upper (left) and lower (right) dentition.

**Description.** Holotype (paratypes): total vertebrae 150 (150–151), predorsal vertebrae 10 (10–11), preanal vertebrae 29 (29–30), precaudal vertebrae 42 (41–43). Lateral line pores before pectoral 5 (5), lateral line pores before dorsal origin 9 (9–11), lateral line pores before level of anus 28 (29–30), dorsal rays before level of anus 51 (47–53), total and anal rays not countable in radiographs. Total length 293 (263–302) mm, standard length 288 (259–298) mm, preanal 35.2 (32.4–33.3)% TL, predorsal 18.8 (16.9–18.5)% TL, head 15.6 (14.3–15.0)% TL, depth at anus 6.7 (5.4–6.5)% TL, snout 21.9 (19.2–22.0)% HL, eye 10.1 (9.8–11.5)% HL, interorbital 16.2 (14.0–16.6)% HL, mouth 27.1 (23.8–28.3)% HL, branchial aperture 16.4 (10.1–16.5)% HL, branchial interspace 28.0 (29.3–34.2)% HL, pectoral 51.0 (43.8–51.0)% HL.

Body elongate but not markedly so, preanal portion rather deep, caudal region narrow and delicate; snout bulbous, broad when viewed from above, underside with complex folds and papillae partly covering anteriormost teeth; lower jaw much shorter than snout, with weak folds; anterior nostril a short tube, subterminal, its rim complete; posterior nostril a simple aperture with a raised rim, placed high on snout well before anterodorsal corner of eye; mouth cleft short, barely reaching to below anterior margin of eye; no significant upper lip, a well-developed lower lip; eye relatively small, round; interorbital broad; branchial aperture vertical, curved, moderately large, its upper extremity placed just below middle of pectoral base; pectoral noticeably very long, narrow, pointed, the base oblique so that fin is directed dorsally; dorsal origin behind branchial aperture, about level with midpoint of pectoral; preanal length about one-third of total; dorsal fin height about one-seventh of body depth; anal fin somewhat lower; caudal fin present; lateral line pores inconspicuous, ending (in holotype) about 40 mm before caudal tip; cephalic pores present, moderately developed, in holotype as follows: in supraorbital canal 1 small (ethmoid) pore on ventral surface of snout, with 2 larger pores anterodorsal to anterior nostril; in infraorbital canal 5 pores close to ventral edge of snout; no postorbital pores, in preoperculo-mandibular canal 2 anterior pores only; no supratemporal pores.

Teeth on maxillary and dentary generally short and bluntly conical, in bands (Figs 3C, 4); on maxillary in 3 rows of about 16 teeth in each, on dentary in 5 rows anteriorly of about 19 teeth in each, those along medial row larger; teeth on 'premaxillary' portion of premaxillary-ethmovomer placed forward of anterior ends of maxillary bands, larger, sharply conical, 12 in the group (in holotype); vomerine teeth molariform, 22 (in holotype) in about 3 longitudinal rows, forming an elongate patch, the anterior 9 or so teeth noticeably smaller and less rounded than those following. Snout plicae and papillae continue between teeth of upper series.

**Colour of holotype.** In alcohol, generally medium-tan grey on upper half of body anterior to anus, this colour continuing ventrally behind anus to cover most of lateral body surface; belly and lower surface of head creamy white; inner surface of branchial aperture dark, the dark colour showing through branchial region; fins creamy white, extreme tail tip dark; parietal peritoneum black. Colour when fresh unknown. Belly and ventral surface of head with numerous small, low papillae, set in depressions, the most ventral papillae in 2 longitudinal rows from anus to throat.

Holotype a maturing male with well developed but not yet folded testes. Condition of holotype: generally good, though body somewhat twisted from original preservation.

**Remarks.** This species is named for the CSIRO Fisheries Research Vessel *Soela* from which the holotype and paratypes were collected and which has contributed substantially to collections of fishes around Australia in recent years. The species name is to be considered a noun in apposition.

The five specimens of *M. soela* were collected in 350 m off the north-east coast of Queensland. Other hauls in this general area revealed a diverse eel fauna including several genera of congrids (*Rhechias*, *Gnathophis*, *Rhynchoconger*, *Bathyuroconger*), *Coloconger*, *Saurenchelys*, *Dysomma* and *Synaphobranchus*. These collections have yet to be studied in detail but could be usefully compared with similar collections made on the continental slope elsewhere (e.g. Mozambique Channel, Philippines, Bay of Bengal). *Macrocephenchelys brachialis* was collected in 670 m in the Macassar Strait (Fowler, 1934) and in greater than 550 m in the Mozambique Channel (Karrer, 1982). Fowler's (1934) description and figure do not properly represent the unique morphology of *M. brachialis*, the only other species of *Macrocephenchelys*. Robins & Robins (1971) redescribed the holotype, emphasising in their figure the complex nature of the plicae and folds of the snout (a feature only barely mentioned by Fowler), and described the osteology from the cleared and stained paratype. Karrer (1982) described a third specimen, again pointing out the unusual morphology of the species. From these redescriptions and my own study of the holotype of *M. brachialis* it is clear that *M. soela* differs markedly from it in morphology, body proportions and meristics. *Macrocephenchelys soela* is essentially a rather robust eel, not greatly elongate or slender (depth of body at anus 19% preanal length, but only 13% in *M. brachialis* – data from Karrer, 1982), the dorsal origin is much further forwards (i.e. over middle of pectoral, but well behind pectoral in *M. brachialis* – data from Robins & Robins, 1971), the branchial aperture is much larger (its upper extremity level with pectoral base, the whole aperture shorter and below pectoral base in *M. brachialis*), the snout folds are much less complex, and the vomerine teeth are more numerous and distinctly molariform, rather than sparse and sharper as in *M. brachialis*. Vertebrae are fewer in *M. soela* (150–151 total, compared with 179–182 in *M. brachialis*) and lateral line pores before anus are also fewer (29–30 versus 33–34), reflecting the generally less attenuated body shape. Finally, none of the previous descriptions mention the numerous, small, surface, possibly sensory structures set in pits which are a feature

of the ventral surface of *M. soela*, nor in my re-examination of the holotype have I identified these. These structures would warrant further study as to their possible function, if any.

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# *Aulohalaelurus kanakorum* n.sp., a New Species of Catshark (Carcharhiniformes, Scyliorhinidae, Atelomycterinae) from New Caledonia

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ABSTRACT. A new catshark, *Aulohahaelurus kanakorum* n.sp., is described from an adult male collected from off south-western New Caledonia. It is the second species in the genus *Aulohalaelurus*, previously restricted to western Australia. The new species is distinct from its allopatric congener, *Aulohalaelurus labiosus* (Waite, 1905), mainly by colour pattern, longer interdorsal space, pelvic-anal distance, shorter prepelvic length, morphology of dermal denticles and higher number of diplospondylous vertebrae. A neotype is also designated for *A. labiosus* (Waite, 1905).

SÉRET, B., 1990. *Aulohalaelurus kanakorum* n.sp., a new species of catshark (Carcharhiniformes, Scyliorhinidae, Atelomycterinae) from New Caledonia. Records of the Australian Museum 42(2): 127–136.

Fowler (1934: 235–237) defined two subgenera of the genus *Halaelurus* Gill, 1862, *Holohalaelurus* (type species *Scyliorhinus regani* Gilchrist, 1922) and *Aulohalaelurus* (type species *Catulus labiosus* Waite, 1905). The diagnosis provided by Fowler for his new subgenus *Aulohalaelurus* was "...labial folds greatly developed, extend along lower jaw nearly to symphysis..." in which folds mean furrows or grooves as suggested by the Greek stem *aulos* meaning grooves. This subgenus was elevated to generic rank by Whitley (1934: 153; 1940: 89) but Bigelow & Schroeder (1948: 198) relegated it to the synonymy of *Halaelurus*, and Compagno (1973) did not mention this genus in his classification of living elasmobranchs. In his revision of the scyliorhinid catsharks, Springer (1979: 35-36) recognised the monotypic genus *Aulohalaelurus* and provided a more detailed diagnosis. Compagno included *Aulohalaelurus* in his revision of the carcharhinoid sharks (1979: 183) and in his catalogue of sharks (1984b: 294) pointed out that the validity of this genus had to be confirmed. In the revised version of his study on the Carcharhiniformes, Compagno (1988: 103–105) recognised the monotypic genus *Aulohalaelurus* and suggested that it is the "...primitive sister group..." of *Atelomycterus*. Both genera were included in the subfamily Atelomycterinae, new rank for Atelomycteridae White (1936) as proposed and defined by Compagno (1988: 98).

Waite (1905) described his species *Catulus labiosus* from a male 620 mm total length (TL) collected off Fremantle, and supposedly deposited in the Western Australian Museum (WAM). Whitley (1934: fig. 1) illustrated

this specimen. McKay (1966) stated that the type of *Halaelurus labiosus* was in WAM, but none of the WAM specimens he listed as "...actual records..." fits with Waite's holotype. Springer (1979) mentioned that the holotype is "...a 620 mm male WAM...", but he gave no catalogue number for this holotype and provided the measurements of another specimen (adult male 540 mm TL, WAM P12020, Point Peron, Fremantle). Compagno (1984b) determined that Waite's holotype is WAM P13253-001. Through the courtesy of Nick Haigh from WAM, I examined this catalogued specimen, but it is an adolescent male of 482 mm TL, not the 620 mm male described by Waite, although the associated label states it is Waite's holotype! Close comparison of this adolescent male with Whitley's drawing (1934: fig.1) caused me to conclude that undoubtedly Whitley drew this specimen which he thought was "...the unique holotype..." of *A. labiosus*. Considering the two thirds natural size drawing of the holotype's head (Waite, 1905: fig.23), it should actually be about 620 mm long. The correct holotype could not be found and the origin of the confusion could not be explained (N. Haigh, personal communication, 1987). The 620 mm adult male (WAM P27184-001) examined by Compagno (1988) was collected in 1981 off Two Rocks, WA. Thus the specimen WAM P13253-001 is herein designated as the neotype of *A. labiosus* (with the agreement of Dr G.R. Allen, Curator of Fishes, WAM). As a result, the new species was compared to Waite's original description, to subsequent descriptions by Garman (1913), Whitley (1934, 1940), Fowler (1941), Stead (1963), McKay (1966), Springer (1979) and Compagno (1984b, 1988), and to three specimens from WAM.

The new scyliorhinid catshark from New Caledonia is assigned to the genus *Aulohalaelurus* on the basis of the following set of characters (as defined by Compagno, 1984b, 1988): supraorbital crests present on cranium above eyes; anterior nasal flaps moderately expanded, well separated from each other and not reaching mouth; nasoral grooves absent; labial furrows very long, upper reaching level of upper symphysis; second dorsal fin about as large as the first dorsal fin.

## Material and Methods

Measurements were taken according to Compagno (1984a, 1988). Vertebral counts were done on radiographs according to Springer & Garrick (1964). These authors recommend to insert a pin at the origin of upper caudal lobe to separate the precaudal from the caudal vertebrae; however, the number of diplospondylous vertebrae were also counted to the origin of the lower caudal lobe to include all the caudal vertebrae and this number is given in brackets. Teeth and dermal denticles were observed with a stereoscopic microscope and by scanning electron microscope. As the new species is known from the holotype only, no dissection was performed to reveal anatomical structure except for the left clasper; however, the pectoral skeleton structure was observed from radiographs. Terminology of clasper components and cartilages is according to Compagno (1979, 1988). Abbreviations for museums and institutions follow Leviton *et al.* (1985).

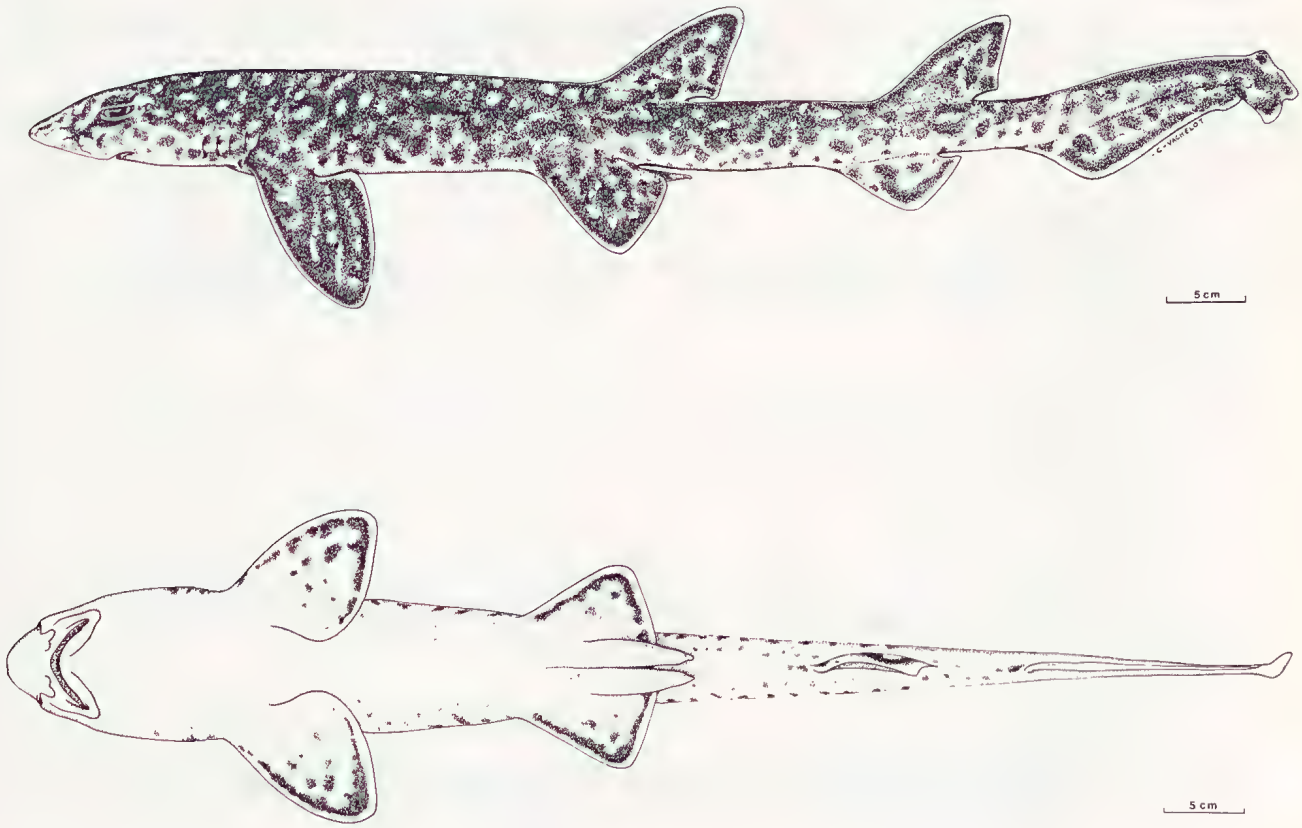
## *Aulohalaelurus kanakorum* n.sp.

Figs 1,2

**Type material.** HOLOTYPE: adult male, 785 mm TL, MNHN 1988.1860, pass of islet N'Do, south-western lagoon off New Caledonia, handlined by Mr Ph. Tirard, 49 m depth, 7 Feb. 1986. (Remark: left mouth corner was torn out, probably when the handline hook was removed).

**Diagnosis** (based on holotype). A relatively small scyliorhinid catshark with the following character combination: body firm, elongate and subcylindrical; head relatively broad and depressed; snout short and rounded in dorsal view and bluntly conical in lateral view; upper and lower labial furrows very long, uppers extending to level of upper symphysis and lowers almost reaching lower symphysis; anterior nasal flaps developed, but not greatly expanded, covering excurrent aperture, separated from each other and falling short of mouth; posterior nasal flaps absent; nasoral groove absent; subocular gutter and ridge present; interdorsal space 1.8 times first dorsal fin base length; pelvic insertion to anal origin interspace 1.9 times anal base length; distance from tip of snout to pelvic origin 2 times head length; dermal denticles with strong medial cusp and barely developed lateral cusp on each side, 2 strong medial ridges and low lateral ridge on each side of crown; colour pattern vivid consisting of numerous dark brown blotches more or less fused to form a variegated brown network surrounding numerous white blotches on back and sides of body; anterior and posterior margins of fins distinctly white and outlined by submarginal dark brown strip. Clasper external components: fused clasper groove, rhipidion, soft rhipidion, cover-rhipidion, exorhipidion, pseudosiphon and pseudopera; clasper glans cartilages: dorsal terminal, ventral terminal, accessory dorsal marginal, dorsal terminal two and ventral terminal two. Diplospondylous precaudal centra 62 (57 to ventral caudal lobe).

**Description.** Morphometric measurements of the holotype are given in Table 1. Body firm with thick and relatively rough skin. Trunk shorter than tail, subcylindrical, with flat belly. Tail elongate, compressed and gently tapering posteriorly, with caudal peduncle short and compressed, vertically oval in cross section. Head short, about 19% TL, relatively broad and depressed, greatest width 1.5 times head length and greatest height at eyes 0.5 times greatest width. Snout short, preoral length 3.2% TL and about 0.4 times mouth width, rounded-parabolic in dorsal view and bluntly conical in lateral view. Nostrils moderately large, with only




**Figs 1 and 2.** *Aulohalaelurus kanakorum* n.sp., adult male 785 mm TL, holotype, MNHN 1988.1860. 1: in lateral view; 2: in ventral view; left mouth corner reconstructed.

small, circular incurrent aperture externally distinct. Anterior nasal flaps triangular lobes with undulated posterior margin, covering excurrent aperture, ending close to the mouth but not reaching it and separated from each other, with internarial width about equal to nostril length. Posterior nasal flaps absent. Nasoral grooves absent. Labial furrows very long; uppers extending to level of upper symphysis; lowers somewhat longer than uppers, almost reaching lower symphysis. Mouth arched, 0.4 times as long as wide, with upper teeth exposed when closed. Tongue and palate without oral papillae but covered with dermal denticles. Eyes elongated ovals, dorsolateral on head, with relatively deep subocular gutters and strong subocular ridges; lower nictating eyelids well differentiated and covered with dermal denticles. Spiracle about one fourth of eye length and close behind eye. Gill slits high, subequal, lateral on head; 4th and 5th slits smaller and over origin of pectoral fin base. External skin of gill slits covered with dermal denticles. Dorsal fins subequal in size and shape, height about equal to base length, with elongate slightly convex anterior margin, bluntly pointed apex, straight posterior and concave inner margin, free rear tip abruptly angular. First dorsal origin slightly anterior to level of pelvic insertion. Interdorsal space 1.8 times first dorsal fin base length. Pectoral fin moderately large, anterior and posterior margins slightly convex, angular apex and broadly rounded inner corner. Pelvic fin with nearly straight anterior and posterior margins, apex as blunted right angle, inner margins not fused to form apron over claspers. Anal fin small, low and triangular, smaller than second dorsal fin and about opposite to it, original of anal base far behind pelvic insertion and slightly anterior to level of second dorsal fin; anterior and posterior margins slightly convex, apex bluntly angular, inner margin short and straight, free rear tip sharply angular. Caudal fin short, about 20% TL, upper caudal lobe poorly developed, upper caudal margin slightly convex, not undulated and without crest of dermal denticles; terminal lobe large, subrectangular with its posterior margin indented as if a result of some abnormality or regeneration subsequent to some injury; ventral lobe elongate and relatively high, preventral margin sigmoid, postventral margin slightly concave, apex bluntly angular; subterminal notch simple deep slot.

Colour pattern of fresh specimen from colour photos vivid consisting of numerous dark brown blotches more

Table 1. Morphometric measurements of *Aulohalaelurus kanakorum* n.sp. and *A. labiosus* , expressed as percentage of total length (TL).

| | *A. kanakorum* MNHN 1988.1860 adult male | *A. labiosus* WAM P13253.001 adolescent male | *A. labiosus* WAM P27957.001 juvenile male | *A. labiosus* WAM P27957.001 juvenile male | McKay, 1966 *A. labiosus* WAM P332 male | McKay, 1966 *A. labiosus* WAM P11749 adult male | Springer, 1979 *A. labiosus* WAM P1202 adult male | *A. labiosus* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Total length in mm | 785 | 482 | 308 | 294 | 487 | 585 | 584 | MEAN | ST.DEV. | N |
| (%TL) | | | | | | | | | | |
| Tip of snout to first dorsal fin | 45.9 | 48.3 | 45.8 | 47.3 | 49.1 | 49.6 | 49.3 | 48.2 | 1.5 | 6 |
| Tip of snout to second dorsal fin | 66.9 | 65.8 | 62.0 | 63.9 | 66.7 | 67.7 | 66.9 | 65.5 | 2.2 | 6 |
| Tip to snout to upper caudal lobe | 81.0 | 80.9 | 78.2 | 78.9 | | | 79.6 | 79.4 | 1.2 | 4 |
| Tip of snout to pectoral origin | 17.2 | 17.0 | 18.8 | 18.0 | 16.4 | 17.3 | 17.8 | 17.6 | 0.8 | 6 |
| Tip of snout to pelvic origin | 39.0 | 41.9 | 41.6 | 42.2 | 42.3 | 43.1 | 43.5 | 42.4 | 0.7 | 6 |
| Tip of snout to anal origin | 61.1 | 59.1 | 56.8 | 59.5 | 62.6 | 63.4 | 63.2 | 60.8 | 2.7 | 6 |
| Tip of snout to lower caudal lobe | 77.1 | 74.7 | 72.7 | 74.1 | 78.0 | 78.8 | | 75.7 | 2.6 | 5 |
| Tip of snout to cloaca | 41.5 | 45.2 | 42.5 | 43.9 | | | 46.3 | 44.5 | 1.6 | 4 |
| Preorbital length | 4.8 | 5.0 | 4.9 | 4.4 | 4.5 | 4.1 | 5.1 | 4.7 | 0.4 | 6 |
| Eye length | 3.1 | 2.9 | 2.6 | 2.7 | 2.5 | 2.4 | 1.9 | 2.5 | 0.3 | 6 |
| Eye height | 1.1 | 1.0 | 1.0 | 1.0 | | | | 1.0 | 0.0 | 3 |
| Interorbital space | 6.2 | 5.6 | 6.0 | 5.8 | 5.3 | 5.6 | 5.7 | 5.7 | 0.2 | 6 |
| Prespiracular length | 8.9 | 8.7 | 8.4 | 8.2 | 7.2 | 7.7 | 8.0 | 8.0 | 0.5 | 6 |
| Spiracle diameter | 0.8 | 0.8 | 0.6 | 0.6 | | | 0.7 | 0.7 | 0.1 | 4 |
| Prenarial length | 2.0 | 1.7 | 2.0 | 2.2 | 1.8 | 1.9 | 2.0 | 1.9 | 0.2 | 6 |
| Nostril length | 2.2 | 1.9 | 2.3 | 2.0 | | | | 2.1 | 0.2 | 3 |
| Internarial space | 2.3 | 2.5 | 2.3 | 2.2 | | | 2.3 | 2.3 | 0.1 | 4 |
| Nasal flap length | 1.7 | 1.7 | 1.9 | 2.0 | | | | 1.9 | 0.2 | 3 |
| Preoral length | 3.2 | 3.1 | 3.2 | 3.1 | 2.7 | 3.1 | 3.1 | 3.1 | 0.2 | 6 |
| Mouth width | 7.3 | 6.5 | 6.5 | 5.8 | 6.4 | 6.3 | 7.4 | 6.5 | 0.5 | 6 |
| Mouth length | 3.2 | 3.4 | 3.1 | 3.1 | | | 3.3 | 3.2 | 0.2 | 4 |
| Upper labial furrow length | 3.4 | 3.5 | 3.1 | 3.1 | 3.1 | 3.4 | 3.7 | 3.3 | 0.3 | 6 |
| Lower labial furrow length | 3.9 | 3.5 | 3.6 | 3.6 | 3.6 | 3.6 | | 3.6 | 0.0 | 5 |
| Pre-first gill slit length | 14.4 | 14.3 | 14.6 | 14.3 | 12.3 | 12.8 | 13.9 | 13.7 | 0.9 | 6 |
| Pre-fifth gill slit length | 19.1 | 18.7 | 19.2 | 18.7 | 17.2 | 18.3 | 18.5 | 18.4 | 0.7 | 6 |
| First gill slit height | 2.4 | 1.8 | 2.3 | 1.8 | | | 2.2 | 2.0 | 0.3 | 4 |
| Fifth gill slit height | 1.6 | 1.1 | 1.3 | 1.4 | | | 1.1 | 1.2 | 0.2 | 4 |
| D1 anterior margin length | 12.0 | 12.4 | 11.4 | 10.5 | | | | 11.4 | 1.0 | 3 |
| D1 base length | 7.5 | 8.3 | 7.0 | 7.3 | 7.0 | 7.5 | 6.9 | 7.3 | 0.5 | 6 |
| D1 height | 7.4 | 6.2 | 6.3 | 5.3 | 5.1 | | 5.6 | 5.7 | 0.5 | 5 |
| D1 inner margin length | 2.9 | 3.0 | 2.9 | 2.4 | | | 3.1 | 2.9 | 0.3 | 4 |
| D1 posterior margin length | 7.0 | 6.0 | 5.0 | 5.3 | | | | 5.4 | 0.5 | 3 |
| Interdorsal space | 13.8 | 9.1 | 9.1 | 10.0 | | | 10.4 | 9.7 | 0.7 | 4 |

Table 1 cont'd: idem.

| | *A. kanakorum* MNHN 1988.1860 adult male | *A. labiosus* WAM P13253.001 adolescent male | *A. labiosus* WAM P27957.0001 juvenile male | *A. labiosus* WAM P27957.001 juvenile male | McKay, 1966 *A. labiosus* WAM P332 male | McKay, 1966 *A. labiosus* WAM P11749 adult male | Springer, 1979 *A. labiosus* WAM P1202 adult male | *A. labiosus* | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Total length in mm | 785 | 482 | 308 | 294 | 487 | 585 | 584 | MEAN | ST.DEV. | N |
| (%TL) | | | | | | | | | | |
| D2 anterior margin length | 11.6 | 12.4 | 12.5 | 10.9 | | | | 11.9 | 0.9 | 3 |
| D2 base length | 7.5 | 9.1 | 9.0 | 8.2 | 7.4 | 7.4 | 8.3 | 8.2 | 0.7 | 6 |
| D2 height | 6.5 | 5.9 | 6.2 | 5.4 | 4.9 | 6.0 | 5.2 | 5.6 | 0.5 | 6 |
| D2 inner margin length | 2.7 | 3.0 | 2.6 | 2.4 | | | 2.8 | 2.7 | 0.3 | 4 |
| D2 posterior margin length | 6.4 | 5.4 | 5.1 | 5.2 | | | | 5.2 | 0.2 | 3 |
| Pectoral anterior margin length | 12.4 | 11.6 | 10.4 | 9.5 | 10.1 | 12.0 | 11.3 | 10.8 | 1.0 | 6 |
| Pectoral base length | 4.8 | 3.8 | 4.2 | 4.4 | 4.3 | 4.4 | 4.3 | 4.2 | 0.2 | 6 |
| Pectoral inner margin length | 5.5 | 5.4 | 3.9 | 4.1 | | | | 4.5 | 0.8 | 3 |
| Pectoral posterior margin length | 10.1 | 8.1 | 8.4 | 7.7 | | | 8.1 | 8.1 | 0.3 | 4 |
| Pectoral insertion to pelvic length | 18.9 | 21.0 | 21.1 | 21.3 | | | 20.4 | 21.0 | 0.4 | 4 |
| Pelvic anterior margin length | 8.4 | 8.7 | 7.8 | 7.1 | 7.2 | 7.7 | | 7.7 | 0.6 | 5 |
| Pelvic base length | 6.4 | 6.4 | 4.9 | 5.2 | 6.0 | 5.5 | | 5.6 | 0.6 | 5 |
| Pelvic length | 10.7 | 10.6 | 8.4 | 8.5 | | | 10.0 | 9.4 | 1.1 | 4 |
| Pelvic inner margin length | 5.1 | 4.6 | 3.6 | 3.6 | | | | 3.9 | 0.6 | 3 |
| Pelvic posterior margin length | 6.6 | 5.9 | 5.9 | 5.8 | | | | 5.9 | 0.1 | 3 |
| Pelvic insertion to anal origin | 16.2 | 13.0 | 13.0 | 12.6 | | | 13.5 | 13.0 | 0.4 | 4 |
| Anal anterior margin origin | 8.0 | 10.0 | 8.1 | 8.3 | | | | 8.8 | 1.0 | 3 |
| Anal base length | 8.5 | 10.4 | 9.1 | 9.5 | 9.2 | 9.4 | 8.1 | 9.3 | 0.7 | 6 |
| Anal length | 10.6 | 12.9 | 11.0 | 11.6 | | | | 11.8 | 1.0 | 3 |
| Anal inner margin length | 2.0 | 2.3 | 1.9 | 2.0 | | | 2.0 | 2.1 | 0.2 | 4 |
| Anal posterior margin length | 5.2 | 3.9 | 4.5 | 4.4 | | | | 4.3 | 0.3 | 3 |
| D2 insertion to lower caudal lobe | 7.4 | 6.6 | 7.0 | 7.5 | | | 4.8 | 6.5 | 1.2 | 4 |
| Anal insert. to lower caudal lobe | 7.4 | 5.0 | 7.1 | 5.4 | | | 6.9 | 6.1 | 1.1 | 4 |
| Caudal peduncle height | 3.4 | 4.0 | 4.2 | 4.4 | | | 3.9 | 4.1 | 0.2 | 4 |
| Caudal peduncle width | 2.1 | 2.6 | 2.9 | 3.2 | | | | 2.9 | 0.3 | 3 |
| Upper caudal lobe length | 17.6 | 19.6 | 22.4 | 21.4 | | | | 21.1 | 1.4 | 3 |
| Lower caudal lobe length | 18.3 | 20.5 | 20.5 | 21.8 | | | | 20.9 | 0.8 | 3 |
| Subterminal caudal lobe length | 3.6 | 2.2 | 3.9 | 3.4 | | | | 3.2 | 0.9 | 3 |
| Clasper outer length | 7.5 | 7.3 | 1.9 | 1.4 | | | | | | |
| Clasper inner length | 11.0 | 10.6 | 4.1 | 4.1 | | | | | | |
| Clasper base width | 1.7 | 1.2 | 0.9 | 1.0 | | | | | | |

or less fused to form variegated brown network surrounding numerous white blotches on back and sides of body; anterior and posterior margins of fins distinctly white and outlined by a submarginal dark brown strip. Venter white to creamy white with few scattered dark brown spots on tail; anterior margin of pectoral and pelvic fins narrowly white, posterior margin markedly white, centre of fins with some scattered dark spots. When exposed to air, faint brownish crossbands appear on back of head and trunk of preserved specimen, one band on head at level of gill slits, one on trunk at level of pectoral fins and one at midtrunk level.

Pectoral fin skeleton (Fig.3, from radiographs) aplesodic, length of greatest radial 47% of anterior pectoral margin length. Total number of radials 16 with 3–4 elements. Propterygium with proximal radial element, intermediate radial element and 2 distal radial elements. Mesopterygium with 3 proximal elements fused at base, 2 rows of intermediate elements and row of distal elements. Metapterygium with row of 12 proximal elements, 1–2 rows of intermediate elements and 0–1 row of distal elements.

**Fig.3.** *Aulohalaelurus kanakorum* n.sp., adult male 785 mm TL, holotype, MNHN 1988.1860, left pectoral skeleton from radiographs.

Cranium not dissected in holotype, but presence of developed supraorbital crests verified by probing and from radiographs.

Teeth (Fig.4) similar in both jaws, those in lower jaw somewhat larger. Teeth arranged in quincunx, with 2-6 series (functional and replacement teeth). Tooth rows in upper jaw 74, with 2/2 medial and 35/35 anteroposterior. Teeth near symphysis typically with strong, erect primary cusp, flanked at base with smaller secondary cusplets. Most teeth tricuspid, with strong primary cusp and smaller secondary cusplets about half size of primary on each side. Some teeth with very reduced secondary cusplet, obliquely orientated, on one or both sides. Outer surface of cusps and cusplets predominantly smooth with few low longitudinal ridges, not reaching tip of cusps. Cutting edges of teeth smooth, without serrations. Medial teeth smaller than anterior ones; size of anteroposterior teeth decreasing from symphysis to jaw articulation. Moderately narrow and deep basal groove separating crown from root. Root consisting of 2 large lobes separated by open transverse groove on attachment surface.

Dermal denticles (Fig.5) observed on upper flank under first dorsal fin. Denticle crown roughly tricuspid with strong twin medial ridges separated by shallow groove, ending in strong pointed medial cusp; wing-like lateral extensions with low lateral ridge ending in very short, blunt, hardly developed cusp. Crown outer surface without microrelief. Crown length about 0.75 mm, width about 0.45 mm. Denticles more or less regularly arranged and spaced.

Total vertebral count (Table 2): 151, including 45 monospondylous precaudal centra (MP), 62 (57) diplospondylous precaudal centra (DP), and 44 (49) caudal centra (DC). Ratios as defined by Compagno (1988):

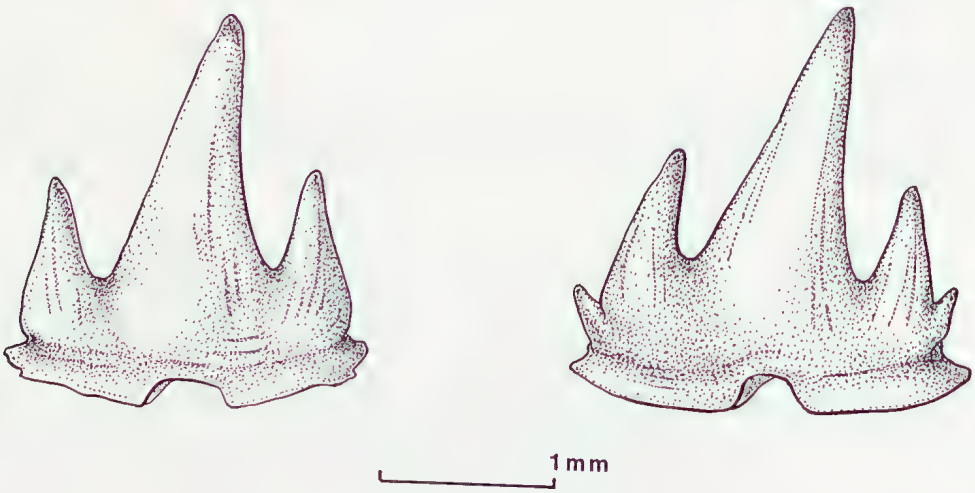



**Fig.4.** Frontal view of anterior teeth of *Aulohalaelurus kanakorum* n.sp., adult male 785 mm TL, holotype, MNHN 1988.1860.

DP/MP = 1.4 (1.3), and DC/MP = 1.0 (1.1).

Clasper morphology (Fig.6a). Claspers stout, moderately long and fairly thick extending to nearly half of their inner length behind pelvic fin tips. Claspers subcylindrical, glans tapering with tips bluntly pointed. Whole ventral surface of claspers covered with dermal denticles extending to outer margin of dorsal surface of ventral lobe, otherwise dorsal surface smooth. Clasper hooks absent. Clasper groove (CG) not open dorsally on proximal part; dorsomedial edges of marginal cartilages united by soft tissue and forming closed tube or fused clasper groove (FCG) between apopyle (APO) and hypopyle (HP). On dorsomedial edge of dorsal lobe of glans, a moderately large cover-rhipidion (CR) with moveable bean-shaped lateral expansion, covering proximal part of rhipidion (RH). Rhipidion (*sensu* Leigh-Sharpe, 1920) large longitudinal blade sustained by cartilaginous element, with base attaching to inner margin of dorsal lobe and with dorsomedial free edge extending laterally from level of hypopyle to distal part of glans. Along inner margin of ventral lobe, a massive dermal component corresponding to 'rhipidion' of rajoid specialists, consisting of soft and thick pseudo-lamellae without cartilaginous structure (this component, left unnamed for sharks by Compagno, 1979, 1988, is herein termed soft rhipidion (SRH) although not being fan-like). Exorhipidion (ERH), differentiated but not greatly expanded, extending from level of hypopyle to distal part of glans on dorsolateral edge of ventral lobe and primarily over soft rhipidion, blade-like, relatively

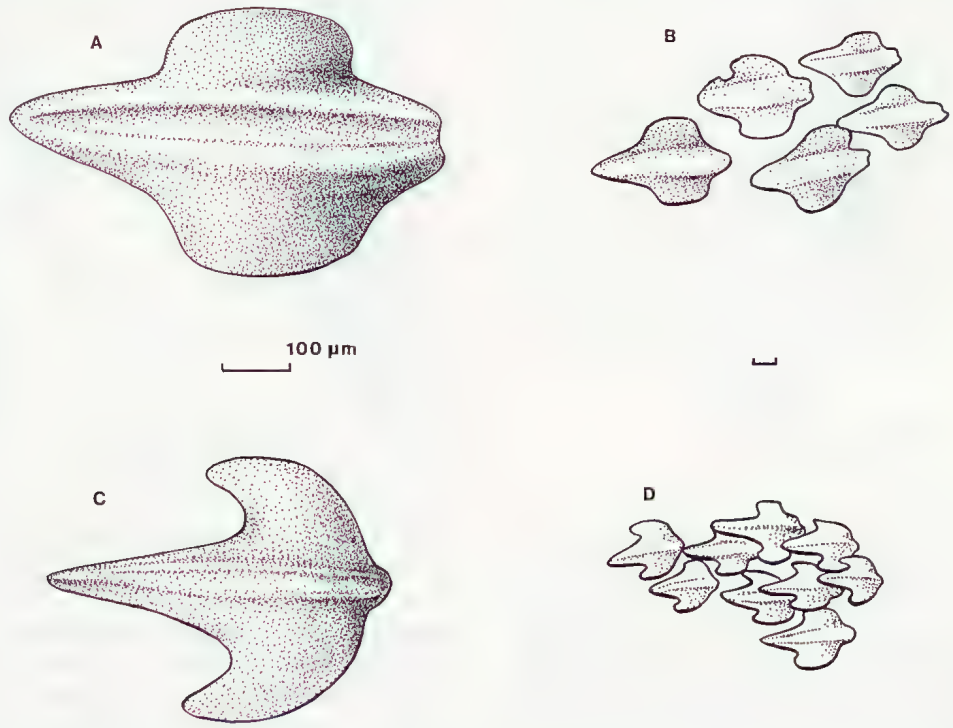



**Fig.5.** Dermal denticles from the upper flank under the first dorsal fin. a,b: *Aulohalaelurus kanakorum* n.sp., adult male 785 mm TL, holotype, MNHN 1988.1860; c,d: *A. labiosus*, adolescent male, 482 mm TL, WAM P13253-001.

Table 2. Vertebral counts and ratios of *Aulohalaelurus kanakorum* n.sp and *A. labiosus*. In brackets: counts and ratios enumerated and calculated with precaudal vertebrae counted to ventral caudal lobe.

| | *A. kanakorum* MNHN 1988.1860 male 785 mm | *A. labiosus* WAM P13253.001 male 482 mm | *A. labiosus* WAM P27957 male 308 mm | *A. labiosus* WAM P27957 male 294 mm | *A. labiosus* Compagno 1988 male 620 mm |
|---|---|---|---|---|---|
| Monospondylous vertebrae MP | 45 | 45 | 45 | 46 | 46 |
| MP in % Total number | 29.8 | 30.4 | 29.8 | 30.9 | 29.7 |
| Diplospondylous vertebrae DP | 62 (57) | 57 (54) | 57 (52) | 57 (51) | 55 |
| DP in % Total number | 41.1 (37.7) | 38.5 (36.5) | 37.7 (34.4) | 38.3 (34.2) | 35.5 |
| Caudal vertebrae DC | 44 (49) | 46 (49) | 49 (54) | 46 (52) | 54 |
| DC in % Total number | 29.1 (32.5) | 31.1 (33.1) | 32.5 (35.8) | 30.9 (34.9) | 34.8 |
| Total number in vertebrae | 151 | 148 | 151 | 149 | 155 |
| DP/MP | 1.4 (1.3) | 1.0 (1.1) | 1.1 (1.2) | 1.0 (1.1) | 1.2 |
| DC/MP | 1.0 (1.1) | 1.0 (1.1) | 1.1 (1.2) | 1.0 (1.1) | 1.2 |

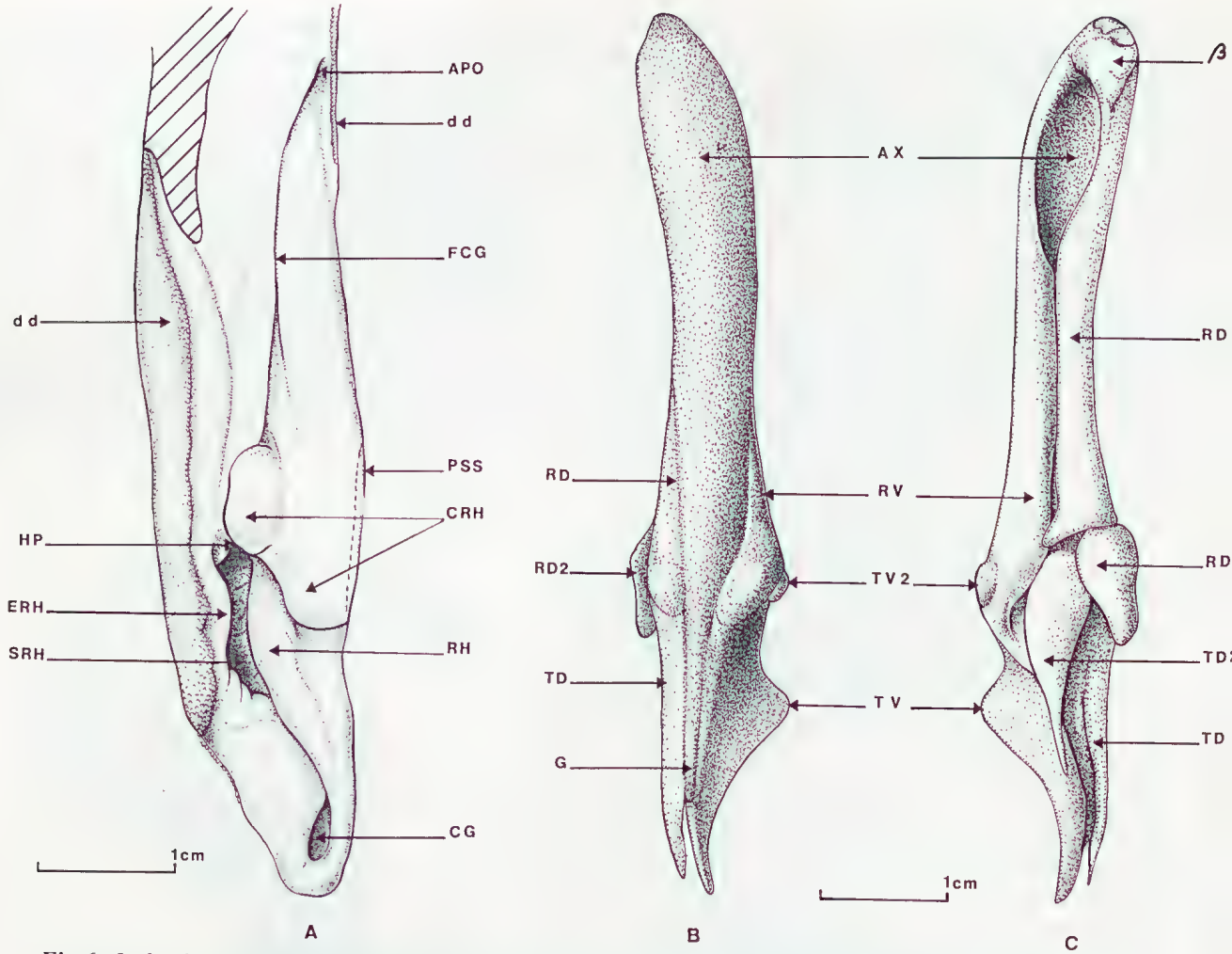



**Fig.6.** Left clasper of *Aulohalaelurus kanakorum* n.sp., adult male 785 mm TL, holotype, MNHN 1988.1860. a: dorsal view; b: skeleton in ventral view; c: skeleton in dorsal view. See text for terminology.

moveable with convex free edge forming root of a blind elongate cavity along inner margin of ventral lobe; pseudopera (PSP) opening laterally, close to hypopyle. Pseudosiphon (PSS) opening along dorsal margin of dorsal lobe, opposite level of cover-rhipidion. Envelope absent on dorsomedial edge of ventral lobe of glans.

Clasper skeleton (Fig.6b,c). Proximal part of clasper skeleton or clasper shaft consisting of axial cartilage (Ax), by means of which clasper attaches to basipterygium of pelvic fin and 2 marginal cartilages, dorsal marginal cartilage (RD) and ventral marginal cartilage (RV). Marginal cartilages curved, tightly fused to Ax along ventromedial edge and joined by soft tissue along dorsomedial edge, forming clasper tube together with Ax. Distal part of Ax or end-style (G), long rod-like, only partially calcified, extending to distal part of glans. Clasper glans skeleton consisting of 5 cartilages. Dorsal terminal cartilage (TD) and ventral terminal cartilage (TV) attaching respectively to RD and RV along their anterior edge, to G along their ventromedial edge and posteriorly united by connective tissue to form clasper tip. Accessory dorsal marginal (RD2) cartilaginous, fingernail shaped, anteriorly articulating to posterior edge of RD, supporting cover-rhipidion. Lateral flap of cover-rhipidion sustained by posteromedial apophysis of RD. Dorsal terminal 2 (TD2) cartilaginous, oblong, thin and blade-like, attachinganteriorly to RD and internally to longitudinal crest of TD. Internal wall of PSS composed of parts of RD, RD2 and TD and external wall not supported by any cartilaginous element. Gutter-shaped posterior margin of RV forming external of PSP. Exorhipidion (ERH) supported by fibrous tissue and small cartilaginous nodule, ventral terminal 2 cartilage, joined to posterior edge of RV.

Weight of preserved specimen: 1535 g.

**Comparison.** The new catshark, *Aulohalaelurus kanakorum*, is evidently very closely related to its allopatric congener *A. labiosus*; however, both species can be distinguished by a set of features. The most distinctive feature is colour pattern. Although *A. labiosus* may present variations in colour, it is predominantly brownish-grey with scattered dark, relatively small blotches (hence its local name of blackspotted catshark) and a few light spots. In *A. kanakorum*, the blotches are larger, more numerous and are fused to form a dark brown variegated network surrounding numerous white blotches. The ventral side of head and belly of both species is whitish to yellowish white. There are obscure dark

saddle-like markings on the back from head to tail in *A. labiosus*; faint brownish crossbands appeared on the back of *A. kanakorum* when exposed to air. The fins of *A. labiosus*, mainly the dorsals, are white-tipped whereas the anterior and posterior margins of fins of *A. kanakorum* are distinctly white and outlined by submarginal dark brown strip. Preserved juvenile specimens and fresh and live specimens of *A. labiosus* (photographed by N. Haigh) are brownish grey with somewhat larger brown-black blotches, those on the flanks surrounding light blotches to form an irregular longitudinal row or pseudo-ocelli, but dark blotches never fuse to form a reticular pattern as in *A. kanakorum*. *Aulohalaelurus labiosus* also has distinct dark saddle-like markings present on the back of the body, a few white spots scattered on body, dorsal fins white-tipped, and pectorals, in some specimens, with whitish posterior margins. This variegated colour pattern looks like that of *Atelomycterus marmoratus*.

Some morphometric measurements are significantly different between the two species. The interdorsal space is longer in *A. kanakorum* than in *A. labiosus*, 13.8% TL versus 9.7% TL (standard deviation = 0.5; n = 4); the pelvic insertion-anal origin interspace is also longer in *A. kanakorum*, 16.2% TL versus 13.0% TL (standard deviation = 0.4; n = 4); the prepelvic length is shorter in *A. kanakorum* than in *A. labiosus*, 39.0% TL versus 42.4% TL (standard deviation = 0.7; n = 6). The caudal peduncle appeared to be more compressed (width 2.1% TL versus 2.9% TL) and less deep (height 3.4% TL versus 4.1% TL) in *A. kanakorum* than in *A. labiosus*. The first dorsal fin and pectoral fin also appeared somewhat larger, but the upper and lower caudal lobes appeared shorter in *A. kanakorum*; however, these differences have yet to be confirmed.

The dermal denticles of *A. labiosus* are clearly tricuspid with a strong pointed primary cusp and a lateral pointed cusp on each side. The number of diplospondylous vertebrae is somewhat higher in *A. kanakorium* than in *A. labiosus*, 62 (57 if centra counted to ventral caudal lobe origin) versus 55–57 (51–54).

A different maximum size might also be attained, the holotype of *A. kanakorum* is 785 mm TL, and the largest specimen (WAM P5690) of *A. labiosus* is 673 mm TL (McKay, 1966; N. Haigh, personal communication).

**Habitat.** *Aulohalaelurus kanakorum* is a coral reef inhabitant known only from the type locality (south-western lagoon off New Caledonia); *A. labiosus* occurs in shallow waters of west Australian reefs. *Aulohalaelurus kanakorum* can be considered a rare species since this shallow water catshark was recently discovered in an area scientifically and recreationally explored for many years. *Aulohalaelurus labiosus* seems relatively common off Western Australia; however, it was not collected during recent trawling surveys off north-western Australia (Gloerfelt-Tarp & Kailola, 1985; Sainsbury *et al.*, 1985) and seems to be restricted to the coast of Western Australia between the Houtman Abrolhos and Albany.

**Etymology.** *Aulohalaelurus kanakorum* is dedicated to the Melanesian people of New Caledonia.

**Comparative material.** *Aulohalaelurus labiosus* (Waite, 1905): WAM P13253-001, adolescent male 482 mm TL, 32°03'S 115°44'E, Fremantle, WA; WAM P27957-001, 2 juvenile males 294 and 308 mm TL, 29°16'S 114°55'E, Port Denison, WA. *Atelomycterus marmoratus* (Bennett, 1830): MNHN 1987-1301, female 676 mm TL, Kep, Kampuchea; NMW 50049, female 401 mm TL, Singapore. *Atelomycterus macleayi* Whitley, 1939: NMW 85670, juvenile female 160 mm TL, Australia.

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# A New Early Devonian Spinose Phacopid Trilobite from Limekilns, New South Wales: Morphology, Affinities, Taphonomy and Palaeoenvironment

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ABSTRACT. *Paciphacops* (*Paciphacops*) *crawfordae* n.sp. is a distinctive spinose phacopid trilobite of late Pragian (Early Devonian) age from the deepwater, dysaerobic Rosedale Shale, Limekilns district, New South Wales. It is characterised by short occipital, genal and intergenal spines on the cephalon, and short thoracic spines on the axial rings and pleurae. Various combinations of such spines are developed in *P.* (*Paciphacops*) *serratus* Foerste (Lochkovian, New South Wales; Ludlovian, Kazakhstan?) and *P.* (*Paciphacops*) *claviger* Haas (Siegenian, Nevada), but the three species cannot be shown to be related.

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In 1969, Elizabeth Crawford collected shelly fossils from temporary exposures of shales belonging to the Rosedale Shale in the Limekilns district, near Bathurst, New South Wales (Fig.1). This collection included the eight known specimens of the new trilobite species which is the focus of this paper.

## Setting and Stratigraphy

The stratigraphic succession in the Limekilns district (Table 1), where the Devonian strata between the Merrions Tuff and the Winburn Tuff (Table 1) have been assigned to the Limekilns Group by Packham (1968), was first mapped and studied by the late L.V. Hawkins (1953). The stratigraphic terminology was established by Packham (1968) and the age of the succession was discussed by Wright & Chatterton (1988). The area lies just inside the eastern margin of the Hill End Trough of Packham (1968), as indicated by the deepwater sedimentary rocks of the Limekilns sequence.

Devonian fossils occur in three units in the sequence, as summarised by Wright & Chatterton (1988, Table 1). The lowest fossils (?late Lochkovian; Wright &

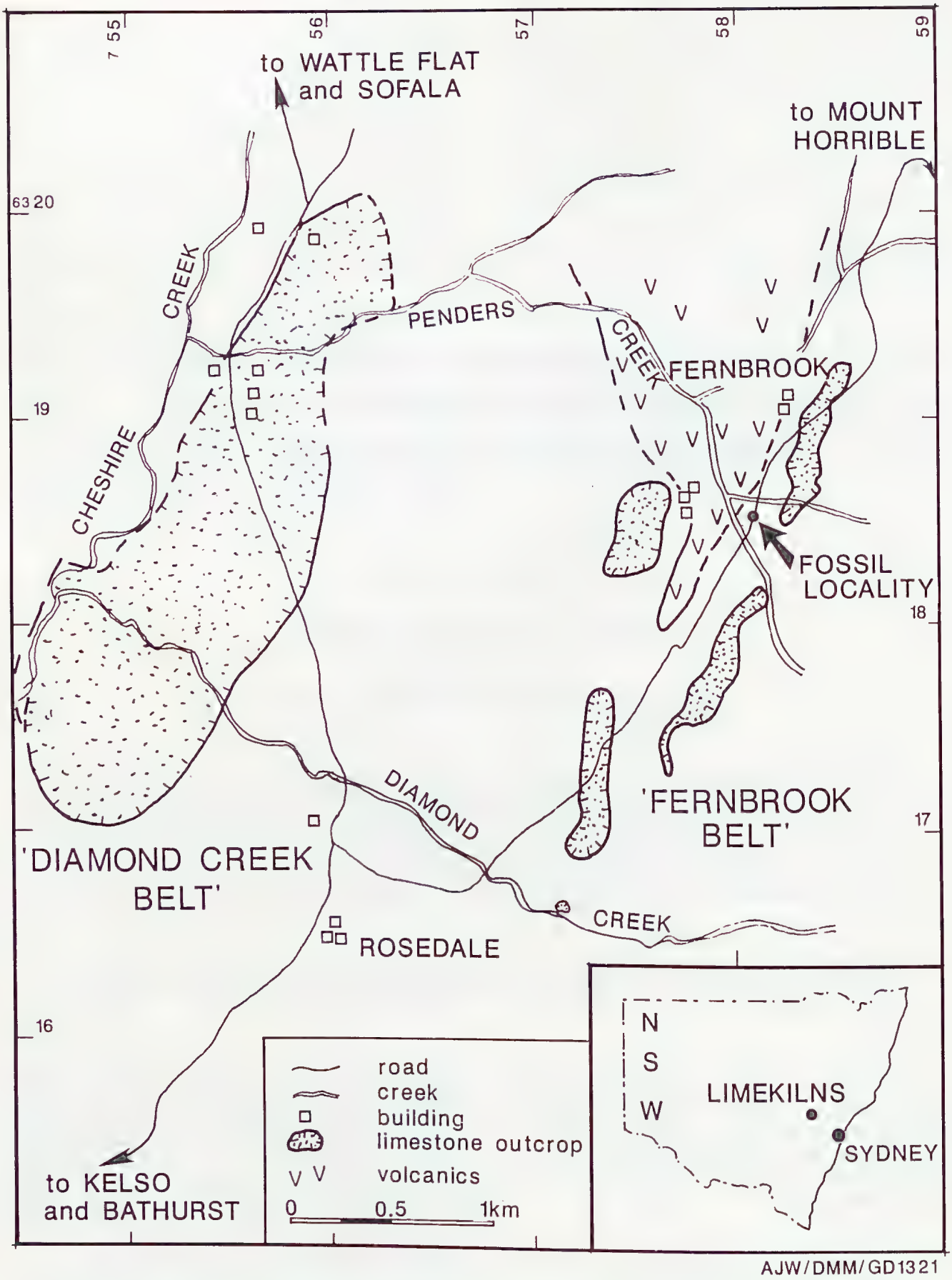


**Fig.1.** Map showing the trilobite locality in relation to limestones of the Diamond Creek and Fernbrook belts and Merrions Tuff as mapped by Stone (1973); base after Bathurst 1:100,000 topographic map 8831 (1st edition, 1975).

Chatterton, 1988; Garratt & Wright, 1988) occur at Paling Yards at the top of the Crudine Group, which is overlain by the unfossiliferous Merrions Tuff.

In the basal unit of the overlying Limekilns Group, the Rosedale Shale (late Pragian; see discussion herein and in Garratt & Wright, 1988), there are scattered fossils, possibly at different levels, and mostly from the Fernbrook belt. Rich faunas occur in the next highest unit, the Jesse Limestone, from the Diamond Creek belt in the western part of the area; the youngest conodonts from this formation indicate a Zlichovian to early Dalejan (late Emsian; discussed herein) age. Trilobites from a level high in the Jesse Limestone were described by Wright & Chatterton (1988). No age-significant fossils are known from the topmost sedimentary unit, the Limekilns Shale which, according to Packham (1968), overlies the Jesse Limestone. Packham (1968) recognised a volcanic unit, the Winburn Tuff, above the Limekilns Group (Table 1).

Despite this apparently simple sequence, some qualifying comments are necessary. At Limekilns, there are two belts of limestone (Fig.1). These are the western or Diamond Creek belt, containing well-preserved and rich faunas, and the eastern or Fernbrook belt, more renowned for its 'marble' quarries (now defunct) than for its well-preserved fossils. These limestone belts outcrop on either side of an expanse of shale (Fig.1); the general structure is believed to be a syncline, but limestone exposures cannot be mapped around the nose of the inferred syncline; as the exposures of the underlying and overlying shales are poor, there are no objective data to prove that the limestones constitute a single formation or occur at a single horizon. In fact, Crawford (1969) recognised limestones at a number of horizons. More recently, studies in the Diamond Creek area by Voorhoeve (1986) indicated that the limestones of the Diamond Creek belt are olistoliths.

## Rosedale Shale: Faunas and Age

The Rosedale Shale yields a mostly pelagic fauna (graptolites, tentaculitids, hyolithids, conulariids) and plant fragments; benthic faunas, mostly brachiopods (notanopliids being possibly epiplanktonic) with some corals, rare bivalves and trilobites, also occur. Strusz (1972) reported *Monograptus yukonensis* (identified by G.H. Packham) from this formation, and inferred a Pragian age.

As stratigraphic control within the poorly exposed Limekilns Group is poor, the relative position and relative age of the trilobite-bearing horizon in the Fernbrook belt and the Jesse Limestone (the source of all the conodont data at hand) in the Diamond Creek belt cannot be established on the basis of mapping. Further, there is the possible need to amend the stratigraphic terminology for the Limekilns district, so that the predominantly shaley sequence (currently termed the Limekilns Group) could be relegated to formation status (Limekilns Formation), containing unnamed limestone olistoliths.

Several palaeontological lines of evidence indicate a late Pragian age for the Rosedale Shale trilobites from the Fernbrook belt: 1) If the trilobites from the Rosedale Shale are at about the *Monograptus yukonensis* level, this would indicate a late Pragian age for the trilobites, according to Lenz (1987, 1988). The occurrence of *M. yukonensis* in the early Zlichovian (see Wright & Chatterton, 1988 *after* Jaeger, 1979) is thus not yet agreed; 2) Most important of all, tenaculitids occurring with the trilobites have been determined by one of us (W.H.) as *Nowakia acuaria*, the well-known Pragian index fossil (e.g. Lütke, 1979); 3) Garratt & Wright (1988) reported the conodont *Polygnathus* cf. *dehiscens* from basal beds of the Jesse Limestone in the Diamond Creek belt, and Wright & Chatterton (1988) referred to this specimen as *P. dehiscens*. Drs R. Mawson and J. Pickett (personal communication, 1987) consider the specimen more likely to be *P. pirenae* Boersma, and it could therefore indicate a late Pragian age for the lower beds of the Jesse Limestone. *Polygnathus pirenae* has been recorded from Limekilns by Mawson *et al.* (1988). Present conodont data from the Jesse Limestone do not conflict with faunal age data from the Rosedale Shale.

The conodont fauna from the upper beds of the Jesse Limestone in the Diamond Creek belt includes (Wright & Chatterton, 1988) *Polygnathus* sp. cf. *P. inversus* and

Table 1. Limekilns sequence (after Packham, 1968) showing approximate positions of fossiliferous horizons and their correlation, as suggested herein and by Wright & Chatterton (1986) and Garratt & Wright (1988).

| Bohemian Stage | Rock Unit | Thickness (m) | Possible Age Range |
|---|---|---|---|
| | Winburn Tuff | 600 | |
| Dalejan | Limekilns Shale | 450 | |
| | | | late Zlichovian – early Dalejan |
| Zlichovian | Jesse Limestone | 60 | |
| | | | late Pragian – early Zlichovian |
| Pragian | Rosedale Shale | 200 | late Pragian |
| | Merrions Tuff | 450 | |
| | | | late Lochkovian |
| Lochkovian | Crudine Group | 750 | |

*Polygnathus* sp. cf. *laticostatus*, of late Zlichovian or early Dalejan age. This did suggest the possibility in the Jesse Limestone of the *pirenae*, *dehiscens*, *perbonus* (= *gronbergi*) and *laticostatus* (= *inversus*) conodont zones of Klapper & Ziegler (1979); however, detailed conodont studies in the district are being carried out by Dr Ruth Mawson and Professor John Talent of Macquarie University, and speculations are clearly hazardous until these studies are further advanced.

## Preservation of Fauna, and Palaeoenvironment

In addition to the eight trilobite specimens, the trilobite locality has yielded only a few benthonic species including several brachiopod taxa (in particular a notanopliid [possibly epiplanktonic] and a leptocoeliid), a few corals and rare bivalves, as well as the 'pelagic' tentaculitids, conulariids and hyolithids.

The closest comparisons appear to be with certain parts of the Siluro-Devonian Melbourne Trough sequence. For instance, the Pragian Wilson Creek Shale contains a pelagic plant-graptolite assemblage; according to Garratt (1983) this lithofacies is restricted to the basin floor in his 'shale lithofacies' which is occasionally pyritic. In the Humevale and Boola Formations Garratt (1983) recognised the *Notanoplia* community of Savage (1974), which may be closer to the Rosedale fauna than is the fauna from the Wilson Creek Shale.

**Taphonomy.** One specimen of *Pac.* (*Paciphacops*) *crawfordae* (AMF 73417) is found as a Salterian moult (Fig.4A) with its thoracopygon intact but slightly disturbed, the hypostoma inverted and displaced (rotated by about 130°) and located under the cephalon which is inverted. The holotype (AMF 73411) consists of a thoracopygon with cephalon nearby (not inverted), and there is another thoracopygon (AMF 73415). All specimens are, to some extent, crushed and deformed by soft-sediment processes, but are not broken or abraded by turbidity or traction currents. Salterian molts cannot to be transported intact by any common mechanism, so the trilobites must be preserved near to their living environment (Speyer, 1985; Speyer & Brett, 1986) and cannot be carcasses of individuals killed by anaerobic or dysaerobic currents.

**Pyritisation.** The trilobite-bearing rocks contain pyrite close to the recrystallised trilobite tests, most of the pyrite being altered to a limonitic (?) mineral. The pyrite is believed to be derived from bacterial decomposition of organic material (Raiswell & Berner, 1985; Dick & Brett, 1986); some oxygenation of the sediments and high initial levels of organic material in the Rosedale Shale are indicated by the abundant bioturbation (e.g. Raiswell *et al.*, 1988). The environment indicated is similar to the dysaerobic one inferred by Thompson & Newton (1987) for the well-preserved, low-diversity *in situ* Late Devonian *Leiorhynchus* fauna of New York which occurs in generally poorly fossiliferous pyritic black shales. Thompson & Newton (1987: 279) argue for "...abundant calcareous fauna..." at "...lower oxygen levels..." than those set by Rhodes & Morse (1971); that is, down to 0.3ml/l $O_2$.

**Depth.** The sparse assemblage dominated by pelagic elements which occurs at places in laminated or bioturbated shales in the formation, together with rare graded sandy turbidites, strongly suggests a deepwater muddy 'outer shelf' or 'continental slope' environment. The shales are occasionally finely bedded and lack the chaotic structure indicative of deposition as slumps. Thus, aspects of both the restricted fauna and the sedimentary rocks demonstrate that the environment was deep and dysaerobic (perhaps episodically, see Wignall & Myers, 1988). If the dysaerobic (see above) interpretation is correct, ponding or some other mechanism may be indicated to account for the reduced oxygenation.

Similar trilobites from similar environments have not yet been described from Australia. The only other Pragian phacopid trilobite described from New South Wales is *Phacops microps* Chatterton, Johnson & Campbell, 1979, but this is a clearly different form from a different biofacies, being from shallow marine carbonates of the Garra Formation. A restricted trilobite fauna of Zlichovian age from the top of the Jesse Limestone described by Wright & Chatterton (1988) not only lacks phacopids, but has a distinctly 'European' aspect.

## Systematic Palaeontology

### Phylum Trilobita

### Suborder Phacopina Struve, 1959

### Family Phacopidae Hawle & Corda, 1847

***Paciphacops* (*Paciphacops*) Maximova, 1972**

**Type species.** *Phacops logani* Hall, 1861 by original designation.

### *Paciphacops* (*Paciphacops*) *crawfordae* n.sp.

Figs 2, 3A–K, 4A–H

**Material examined.** HOLOTYPE, AMF 73411a-b; PARATYPES, AMF 73410a-b, AMF 73412a-b, AMF 73413, AMF 73414a-b, AMF 73415, AMF 73416a-b, AMF 73417a-b. All are from the late Pragian Rosedale Shale, at Limekilns, New South Wales. Grid reference 581185, Bathurst 1:100,000 topographic sheet 8831. All material is deposited in the Australian Museum, Sydney.

**Derivation of name.** The species is named for

Elizabeth Crawford, collector of the described material.

**Diagnosis.** *Paciphacops* (*Paciphacops*) with short, stout occipital, genal and intergenal spines on cephalon, and spines on thoracic axial rings and pleurae. Axial furrow in front of S1 diverging at 75°–90°. Small, anteriorly-placed eye with 11 or 12 vertical files and from 48–57 lenses. Pygidium with about 8 axial rings and up to 5 straight pleural furrows.

**Description.** Cephalon transverse, with prominent overhanging sub-pentagonal glabella. Axial furrows deep and diverge at 75°–90° in front of S1, so that ratio of maximum to minimum glabellar width (tr.) is up to 1:2.25. L1 not as long (exsag.) as median part of occipital ring; L2 at least as long (sag.) as occipital ring. Occipital furrow shallow medially, S1 almost absent medially; both are incised laterally and swing forward laterally; posterior branch of S3 arcuate, anterior branch straight and almost parallel to axial furrow. Facial suture indistinguishable. Sculpture of glabella and posterior parts of fixigenae poorly preserved, consisting of tubercles. Posterior border furrow long (exsag.), shallow and basally rounded, swinging anteromedially well inside genal angle, deepening lateral to eye and again at junction with axial furrow; very shallow but persistent preglabellar furrow. Cephalic doublure broad (sag.) anteriorly. Vincular furrow well defined beneath border, becoming deeper and notched on both sides laterally, with about 8 notches. Short, stout occipital, intergenal and genal spines present.

Palpebral furrow faint to absent; deep furrow below elevated, reniform eye developed posteriorly; weak furrow developed just above the lenses. Eyes small and low, with 11 or 12 files; posterior end located just anterior of S2, anterior end located just in front of abaxial end of S3 and very close to both axial and border furrows. Sclera depressed and narrow below lenses, and thin where seen in internal moulds. Lens composition (Fig.3) can be confidently interpreted in only a few specimens, as follows:-

| | | | |
|---|---|---|---|
| AMF73411 | (ant.) | 45564544443 (post.) | Total lenses:–48 |
| AMF73416 | | 356564664543 | Total lenses:–57 |
| AMF73417 | | 345555544443 | Total lenses:–51 |

AMF 73410 (Fig.3J) and AMF 73416 have irregular lens arrangement at about midlength of eye. The difference in lens number between AMF 73411 (Fig.3A) and AMF 73416 (Fig.4G) does not appear to be size related, as the specimens are of similar size. AMF 73410 has 54 (?plus 2) lenses and 11 or 12 files, but is deformed and difficult to interpret. Hypostoma rather broad, with wide, gently convex forward anterior margin, acute anterior wings, convex, relatively short (sag.) oval middle body with posterior median depression of possible tectonic nature; border furrow present; 3 small posterior spines.

Thorax with prominent spines on axial rings, and on posterior pleural band just lateral to articulation point. Pleural furrows narrow (exsag.), trend obliquely across the pleurae, and extend from near wide (tr.) but poorly defined axial nodes (not completely isolated by notches) to upper part of spatulate facet. Pleurae apparently taper steadily in width (tr.) from cephalon to pygidium.

Pygidium transverse, with about 8 axial rings and a terminal piece, and up to 5 pleural furrows. Axis high and narrow, tapering slightly to ring 5, then tapering more rapidly towards the terminal piece. Axial rings longer (sag.) than narrow (sag.) ring furrows, only 5 of which are developed. Axial furrow weak over anterior few pleurae; strong concentric-forwards apodemes on the first few segments extend from axial furrow on to side of axis. Pleural furrows shallower and narrower than interpleural furrows, producing a smaller posterior portion of the pleurae which expand weakly and curve only slightly, so that the posterior pair of pleurae make an angle of about 30°–40° with the axis. Doublure narrow (sag.), almost horizontal. Border wide (sag.) and smooth, width constant.

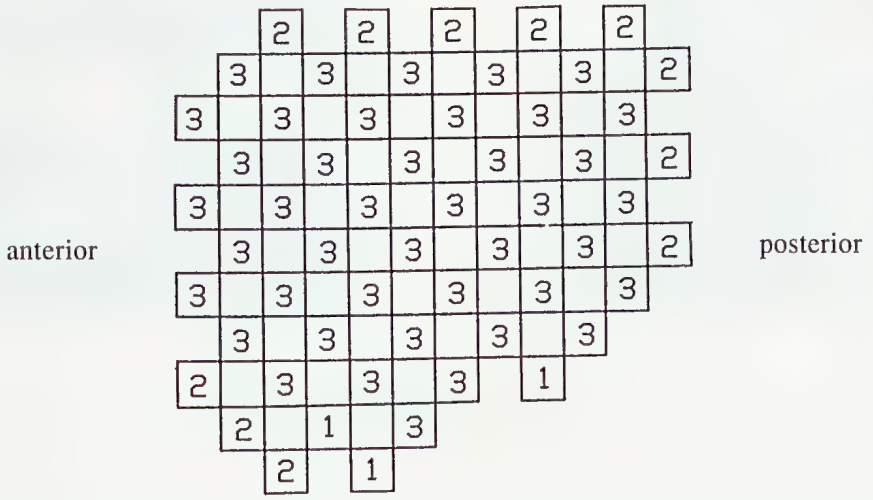


**Fig.2.** Pattern of lenses in eyes of 3 specimens of *Paciphacops* (*Paciphacops*) *crawfordae* (see Campbell, 1977: fig.11).

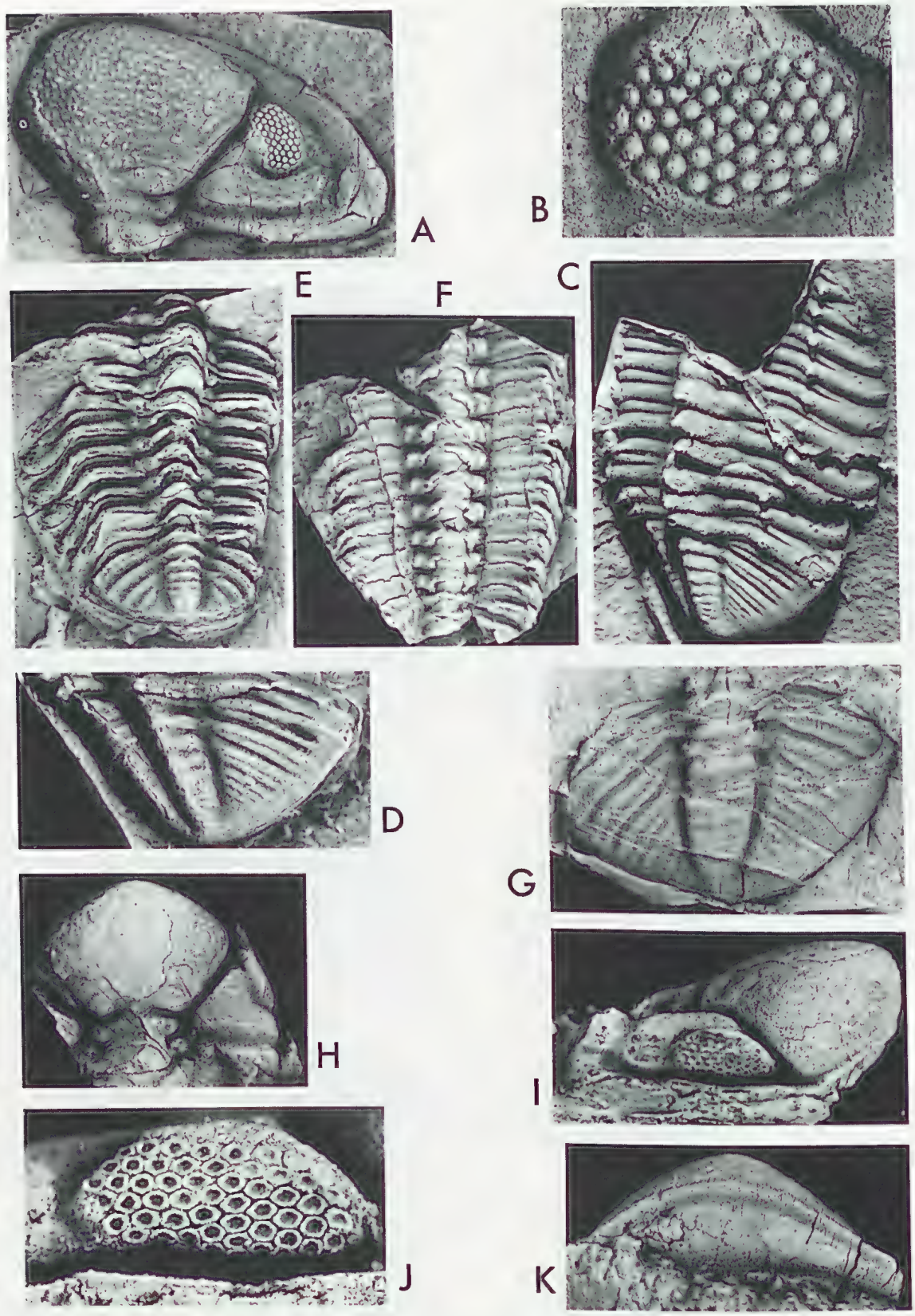


**Fig.3.** A-K: *Paciphacops* (*Paciphacops*) *crawfordae* n.sp., all from Rosedale Shale (late Pragian), Limekilns district, New South Wales. A-D, holotype AMF 73411. A, latex cast of cephalon showing occipital and intergenal spines, x2.5. B, latex cast of eye (anterior to right), x10. C, latex cast of thorax (showing spines) and pygidium, x2.5. D, latex cast of pygidium, x3. E, paratype thoracopygon AMF 73415, internal mould, x2. F, paratype partly testiferous thorax AMF 73413, x1.5. G, paratype pygidium AMF 73414, latex cast, x3. H–K, paratype cephalon AMF 73410. H, latex cast, dorsal view, x2. I, cephalon in anterolateral view, x3. J, internal mould of eye (anterior to right), x8. K, doublure showing continuous vincular furrow, x3.

Dimensions (approximate):-

| | | | |
|---|---|---|---|
| AMF73410 | (cephalon) | length 15.5mm, | width >28mm |
| AMF73411 | (cephalon) | length 14mm, | width 34mm |
| | (thorax) | length >20mm | |
| | (pygidium) | length >11mm | |
| AMF73412 | (cephalon) | length 12mm, | width 26mm |
| AMF73413 | (thoracopygon) | length 26mm, | width 23mm |
| AMF73414 | (pygidium) | length 14mm, | width 21mm |
| AMF73415 | (thoracopygon) | | |
| | pygidium | length 8.5mm, | width 15mm |
| | thorax | | width 17mm |
| AMF73416 | (cephalon) | length 11.5mm, | width 28mm |
| AMF73417 | (hypostoma) | | |
| | body | length 5.5mm, | width 4.5mm |
| | wings | >10mm | |

**Generic assignment.** Although this material is poorly preserved by comparison with many Silurian and Devonian phacopids and details of the sculpture are obscure, a firm generic assignment can be made. One of the characteristics of *Paciphacops* (*Paciphacops*) is the presence of perforated glabellar tubercles in large-eyed forms (Campbell, 1977), but perforations are not visible in the glabellar tubercles in this small-eyed form. Campbell (1977) placed emphasis on the continuous vincular furrow, the thickened sclera in small-eyed forms (in particular) and the straight or slightly convex hypostomal suture as diagnostic characters of this subgenus. Chlupac (1971, 1972, 1977) synonymised *Paciphacops* (*Paciphacops*) and *Paciphacops* (*Viaphacops*), treating *Paciphacops* as a subgenus of *Phacops*, but noted the importance of the continuous vincular furrow. Chlupac (1977) further considered that, in *Phacops* (*Paciphacops*), S1 is weak or interrupted medially, and genal spines are commonly developed; these latter features can be seen in both *Pac. (Pac.) logani* (Campbell, 1977) and *Pac. (Pac.) crawfordae*. Holloway (1980) regarded *Paciphacops* as a synonym of *Ananaspis*, and *Viaphacops* as an independent genus. Holloway & Neil (1982) stated that the only features distinguishing *Paciphacops* from *Ananaspis* are the perforated glabellar tubercles in large-eyed morphs, and the thickened sclera in all small-eyed morphs and most large-eyed morphs. *Paciphacops* (*Angulophacops*) Maximova, 1978, based on *Phacops angulatus* Maximova (1968: 66, pl.20, figs 1–4), was differentiated from *Pac.* (*Paciphacops*) by Maximova (1978: 120) on the basis of the "...triangular sub-cranidial (= vincular) furrow and the corresponding pygidial outline..."

This Limekilns species is assigned to *Paciphacops* (*Paciphacops*) because of the anteriorly continuous and posteriorly notched vincular furrow, the wide and gently convex anterior border and three posterior spines of the hypostoma, and the medially weak S1.

The generic assignment of comparable species should now be discussed. *Phacops claviger* Haas, 1968 was assigned to *Ananaspis* by Holloway & Neil (1982), but the perforated glabellar tubercles (which can be seen on calcareous specimens but not on silicified specimens) and other characteristics (listed in the previous paragraph) suggest that it belongs to *Pac.* (*Paciphacops*). *Phacops serratus* Foerste, 1888 was assigned to *Ananaspis* by Campbell (1967) and Holloway & Neil (1980), and to *Pac.* (*Paciphacops*) by Campbell (1977). In our opinion this species falls outside *Ananaspis* as it possesses a vincular furrow which is clearly continuous across the anterior part of the doublure, and the species is here assigned to *Pac.* (*Paciphacops*).

**Comparisons.** Few other phacopids have spines developed to a significant degree. The most striking of these are *Pac.* (*Paciphacops*) *serratus* and *Pac.* (*Paciphacops*) *claviger*. Spines are also developed in the *cristata* group (Eldredge, 1973; Campbell, 1977) where they "...are variably developed in related taxa and *may not* (our italics) be of much taxonomic value...(and) are probably sexually dimorphic features..." (Campbell, 1977: 33). The *cristata* group belongs to *Paciphacops* (*Viaphacops*) which is not closely related to the species from Limekilns. There are no substantial differences between the eyes of Limekilns specimens which might suggest dimorphism as discussed for other phacopids by (Clarkson, 1966; Campbell, 1977).

*Paciphacops* (*Paciphacops*) *claviger* differs from *Pac. (Pac.) crawfordae* in having a greater number of pygidial pleural furrows, pseudo-half rings on the pygidial axis, spines on alternating thoracic axial rings, larger eyes with 17 vertical files, granules on the tubercles, and a prominent facial suture.

*Paciphacops* (*Paciphacops*) *serratus* differs from *Pac. (Pac.) crawfordae* in many features, including the posterior location of the large eye (14–17 files, 61 lenses), the strong palpebral furrow, the facial suture described by Sherwin (1972), the moderately deep anterior vincular furrow, the spines on some pygidial axial rings, and the absence of genal and intergenal spines. There is some suggestion that the anterior 3 or 4 pygidial axial rings in *Pac. (Pac.) crawfordae* bear transverse elevations, but no nodes or spines have been observed.

Balashova (1968: 206–207, pl.54, figs 1a,b, 2) erected *Reedops serratus spiniferus* for a Ludlovian form from central Kazakhstan. The illustrated material has a small anteriorly placed eye having about 12 vertical files each having six lenses, a stubby occipital spine and apparently a short genal spine as seen in *Pac. (Pac.) crawfordae*, but no definite intergenal spine. This taxon is probably best viewed as another spinose *Paciphacops* but it may be close to *Pac. (Pac.) crawfordae*; as *Pac. (Pac.) serratus* lacks a genal spine, Balashova's specific assignment of this material is suspect. Many described Russian and Chinese phacopids are apparently known only from internal moulds, and external surfaces are crucial for the recognition of spines. A second Russian form, described by Maximova (1968: 84–85, pl.12, figs 7, 8a) as *Reedops* aff. *sternbergi*, appears to have an intergenal spine.

A further *Pac.* (*Paciphacops*) specimen (AMF73418a-b) has recently been collected at Queens Pinch, near Mudgee, NSW, from the Warratra Mudstone (Wright, 1966; Offenberg *et al.*, 1968) which is a deepwater unit dominated by a pelagic fauna (of slightly different aspect to that of the Rosedale Shale) and overlain by the mid-Zlichovian Sutchers Creek Formation yielding

*Polygnathus perbonus*. The generic assignment is based on the weakly continuous anterior vincular furrow and a few apparently perforated glabellar tubercles; S1 is poorly preserved. This incomplete and crushed specimen (Fig.5A–C) differs from *Pac. (Pac.) crawfordae* in having a genal spine placed more medially, a possible intergenal node, and a distinct facial suture. The eye has 11 vertical files and 54 lenses (ant. 3, 5, 5, 6, 6, 6, 6, 5, 5, 4, 2), a similar number to *Pac. (Pac.) crawfordae*. This specimen is different from *Pac. (Pac.) crawfordae*, but seemingly similar to it, and offers some support for the contention that the spinose condition of these phacopids was an

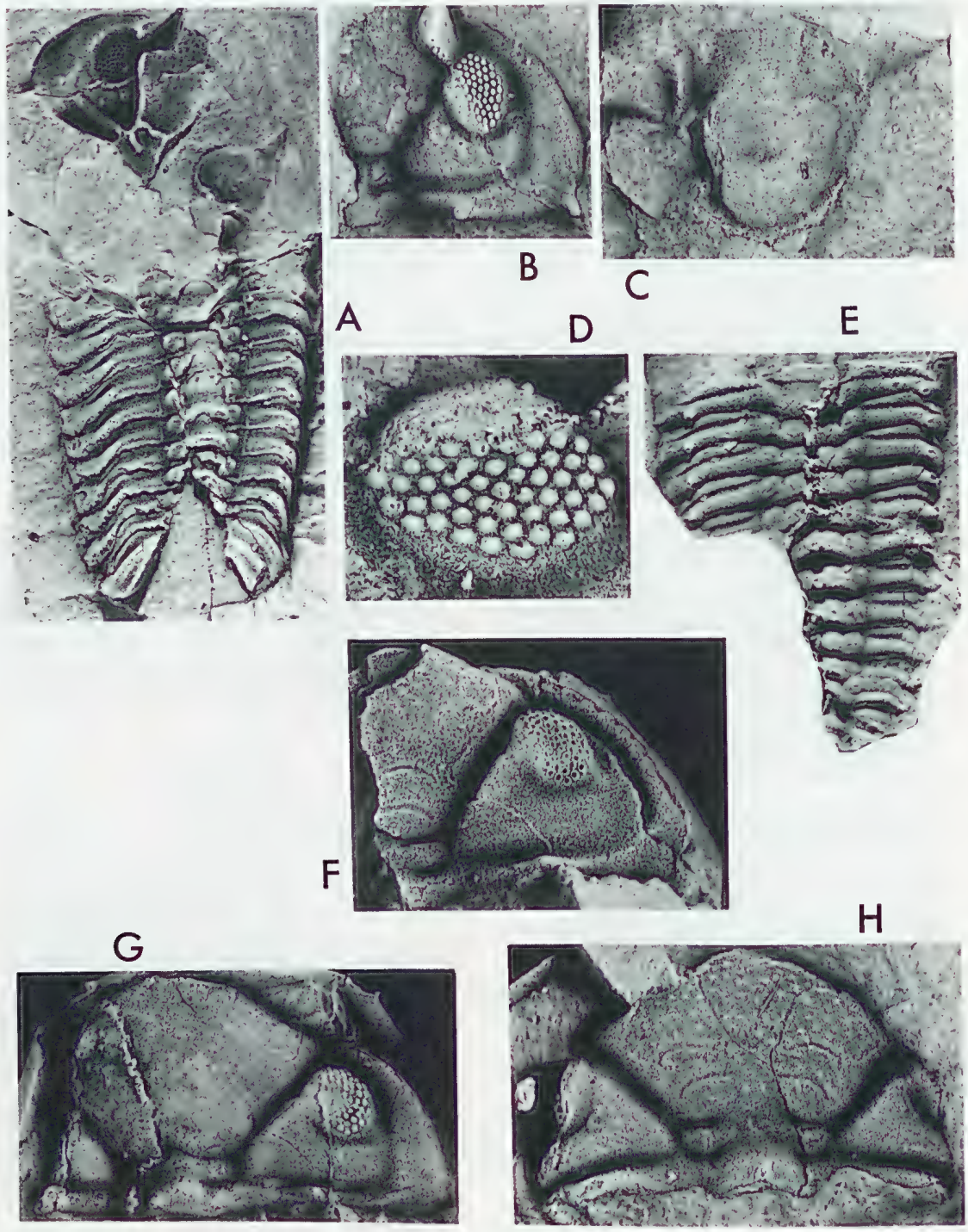


**Fig.4.** A-G: *Paciphacops* (*Paciphacops*) *crawfordae* n.sp., all from the Rosedale Shale (late Pragian), Limekilns district, New South Wales. A-E, Paratype AMF 73417A, A, dorsal view of Salterian molt, with cephalon and hypostoma inverted, x2. B, latex cast of cephalon, showing genal and intergenal spines, x3. C, latex cast of hypostoma, x6. D, latex cast of eye (anterior to right), x10. E, latex cast of thorax showing spines, x2. F-G, paratype cephalon AMF 73416. F, internal mould showing genal spine and vincular furrow, x3. G, latex cast showing occipital and intergenal spines, x3. H. Paratype cephalon AMF 73412, latex cast showing glabellar furrows, x3.

adaptation to a deepwater environment. Available conodont data indicate different ages (Zlichovian, contrasted with late Pragian) for the two occurrences. However, both are in deepwater muds overlain by calcareous units containing abundant allochthonous limestone blocks; thus, reworked blocks could be yielding conodonts indicating only maximum ages.

**General comments on some Australian phacopids.** One of the above species (*Phacops serratus*) was revised by Sherwin (1972) along with other species described from New South Wales by Etheridge & Mitchell (1896) and Fletcher (1950). Victorian species of ?Siluro-Devonian age include the poorly known forms *Phacops sweeti* (Etheridge & Mitchell, 1896: 487, pl.38, fig.9; pl.39, figs 1–2; pl.40, fig.10) and *Phacops mansfieldense* (Etheridge & Mitchell, 1896: 501, pl.39, fig.12). Other Phacopidae described from eastern Australia, with ages suggested herein or by the original authors, include *Phacops* n.sp. (Talent, 1963: 106, pl.75, figs 1–6; pl.76, figs 1–8), Pragian; *Phacops* n.sp. B (Talent, 1963: pl.76, fig.10), Pragian; *Denckmannites rutherfordi* Sherwin (1969), Pridolian; *Phacops spedeni* Chatterton (1971), early Zlichovian; *Paciphacops* (*Paciphacops*) *microps* Chatterton, Johnson & Campbell (1979), Pragian; *Phacops serratus* (Foerste, 1888); (Holloway & Neil, 1980; Talent, 1965), latest Pridolian to early Lochkovian; *Reedops* n.sp., Jell & Holloway (1983), Pridolian; *Phacops* (*Phacops*) sp., Chatterton & Wright (1986), Zlichovian; and *Ananaspis ekphyma* Wright *in* Jones *et al.* (1986), Lochkovian. For the Late Silurian species, in particular, there is considerable disagreement concerning generic and subgeneric assignment (Sherwin, 1972; Campbell, 1976: fig.6); Strusz, fig.20 *in* Jenkins, 1986).

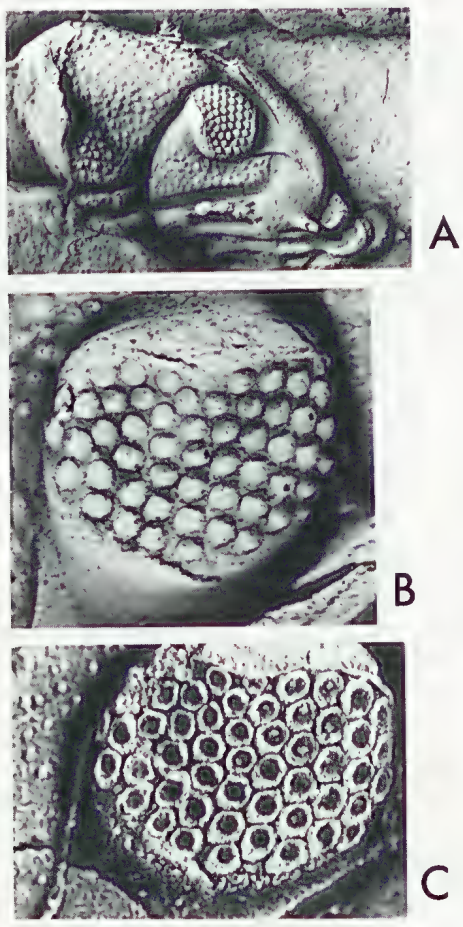


**Fig.5.** A–C: *Paciphacops* (*Paciphacops*) sp., Warratra Mudstone (Zlichovian), Queens Pinch district *via* Mudgee, New South Wales, AMF 73418. A, latex cast of exterior showing genal spine, x3. B, latex cast of eye (anterior to right), x10. C, internal mould of eye (anterior to right), x10.

It is possible that *Pac. (Pac.) serratus* (Pridolian-Lochkovian), *Pac. (Pac.) claviger* (Siegenian), *Pac. (Pac.) crawfordae* (Pragian) and the form from the Warratra Mudstone discussed and figured here are related, and form a compact group which is spinose to a degree not seen in other stocks of phacopids. With so few occurrences a new genus cannot be justified, especially as some of the differences between the three taxa are substantial. Both Eldredge (1973) and Campbell (1977) caution that such spines are of uncertain taxonomic value, and we have no reason to dispute this. For instance, a prominent occipital spine is developed in a probably unrelated Middle Devonian species (*Geesops battidohmi* Struve, 1982).

With regard to a pattern in East Australian Early Devonian phacopids, Chatterton, Johnson & Campbell (1979) stated that *Phacops spedeni* is a 'late *Paciphacops*' transitional to true *Phacops* in having a long L1 and perforated tubercles, and a similar doublure ornament to *Pac. (Pac.) microps*. If so, spinosity may have been an early random trend seen in the Lochkovian *Pac. (Pac.) serratus* and the Pragian *Pac. (Pac.) crawfordae* which was reversed or at least absent in the Pragian *Pac. (Pac.) microps* (which has juvenile genal spines and an adult genal node) and the Zlichovian *Pac. (Pac.) spedeni* (no spines). Preservation does not permit evaluation of the position of *crawfordae* in any morphocline based on criteria relating to tubercles or ornament, as discussed by Chatterton, Johnson & Campbell (1979: 819). Dimorphism is not known in *Pac. (Pac.) microps* or *Pac. (Pac.) spedeni*, but may be present in the *serratus-crosslei* complex (Etheridge & Mitchell, 1896), as the latter two taxa differ only in the absence of thoracic and pygidial axial spines in *Pac. (Pac.) serratus*.

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# Amphipoda from the South Pacific: the Cook Islands

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ABSTRACT. Thirty species of gammaridean Amphipoda from 0 to 1.25 m depth are recorded from the Cook Islands. One species, *Colomastix murivai* n.sp., is new to science and is described and figured. *Perioculodes aequimanus* (Kossman), recorded for the first time from the Pacific, is also figured along with partial figures of four other species of taxonomic interest. The amphipod fauna of the Cook Islands is most closely similar to that of the Society Islands.

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Collections of gammaridean Amphipoda from 0 to 1.25 m depth were made by the writer in 1986 at Rarotonga in the Cook Islands. Two further samples from Rarotonga and one from Mangaia were also studied from the collections of the Smithsonian Institution, Washington D.C., through the kindness of Dr J.L. Barnard. There appear to be no previous records of marine gammaridean amphipods from the Cook Island archipelago.

Thirty species were recorded of which one, *Colomastix murivai* n.sp., is new to science and one, *Perioculodes aequimanus* (Kossman), is new to the Pacific. One species, *Elasmopus takamotus* Myers, was previously known only from Niue (Myers, 1986a).

The Cook Island amphipod fauna shows close affinity with that of the Society Islands to the east (Table 1), but also has a strong component in common with the islands of the Vanuatu–Tonga Island arc and affinity with the island of Nuie. In contrast, only 23% of the Cook Island species recorded herein are known also from Hawaii and all of those except one, have wide Indo-Pacific distributions. Even the exception, *Podocerus talegus* Barnard, is also known from Fiji and Micronesia.

*Colomastix murivai* n.sp., *Periculodes aequimanus* (Kossman), previously unknown from the Pacific, and four other species, *Mallacoota nananui* Myers, *M. subcarinata* (Haswell), *Maera serrata* Schellenberg, and *Podocerus talegus* Barnard, are all described and figured. A list of all material studied in the present work is provided.

Abbreviations used in the figures are as follows: A2 – Antenna 2; Mxp – Maxilliped; P3-6 – Pereopods 3-6; G1, G2 – Gnathopods 1, 2; U1-3 – Uropods 1-3; T – Telson.

## *Colomastix murivai* n.sp.

Fig. 1

**Type material.** HOLOTYPE, female, 2.1 mm, 7 slides. AM P39309, Rarotonga, 2.5 km south of Aorangi, in coral rubble from reef crest, 12 Nov. 1986.

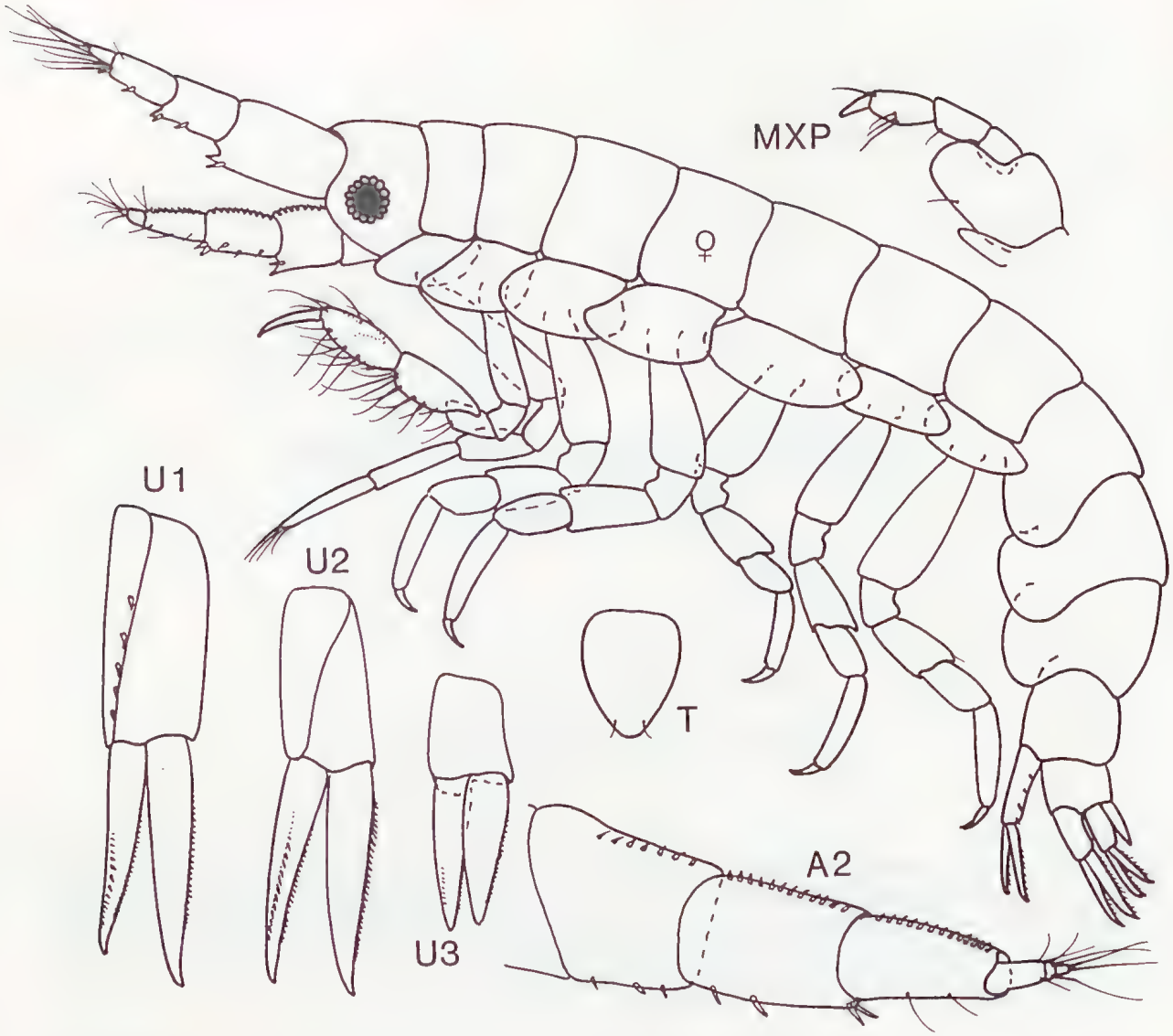


**Fig.1.** *Colomastix murivai* n.sp. Female, 2.1 mm, Rarotonga.

**Description.** Length 2.1 mm. Antenna 1 shorter than combined length of head and pereon segments 1–3, peduncular articles in the basi-distal ratio 9:5:5, articles 1 and 2 with strong posterodistal teeth. Antenna 2 shorter than antenna 1, peduncular article 3 with strong posterodistal tooth, peduncular articles 3–5 each with a dense row of short spines on the anterior margin. Maxilliped outer plate with posterior lobe broad, reaching midway along palp article 2. Gnathopod 1 of normal *Colomastix* form. Gnathopod 2 carpus and propodus subequal, propodus elongate-ovoid. Pereopods 3–7 unarmed. Epimera 1–3 rounded. Uropod 1 peduncle with spines on outer margin, outer ramus a little shorter than inner, inner ramus a little longer than peduncle. Uropod 2 peduncle unarmed, rami subequal and more than three quarters length of peduncle. Uropod 3 stout, rami subequal about one and a half times length of peduncle. Telson longer than broad with a pair of subdistal setae.

**Remarks.** *Colomastix murivai* n.sp. is very close to *C. truncatipes* Ledoyer (1979), but differs in several ways. Antenna 2 articles 3–5 each bears a dense row of small spines on the anterior margin, whereas in *C. truncatipes* the anterior margin of these articles lacks spines completely. The posterior lobe of the outer plate of the maxilliped is broader and extends further forward (to the midpoint of palp article 2) than in *C. truncatipes*. The peduncle of uropod 2 is fully three quarters the length of the rami whereas in *C. truncatipes* it is only a little over one half the length of the rami, and the telson bears subdistal setae, lacking in *C. truncatipes*.

**Distribution.** Currently known only from Rarotonga.

**Etymology.** Named after a river on Rarotonga which embouches near the type locality.

### *Perioculodes aequimanus* (Kossman)

Fig. 2

*Oedicerus aequimanus* Kossman, 1880: 130, pl.13, figs 6–8.
*Perioculodes aequimanus* Schellenberg, 1928: 641, fig.200.

**Remarks.** The original description and figures of this species are very imprecise, but indicate very elongate, subequal, gnathopods 1 and 2. Schellenberg (1928) provides more detailed figures of the gnathopods of material from Suez which he identifies with *P. aequimanus* on the basis of locality (Schellenberg believed the type locality to be Suez) and length. The gnathopods figured by Schellenberg (1928) are much less elongate. Present material appears to be synonymous with that of Schellenberg (1928) and is attributed to Kossman's species even though that species remains equivocal. Should a second species be found in the Red Sea which more closely approximates *P. aequimanus* Kossman than Schellenberg's and present material, then a new taxon will be required for the latter two materials. *Perioculodes aequimenus mozambicus* Ledoyer (1986) differs from the nominate form in its gnathopod 1 and 2 which are strongly dissimilar. Madagascan material probably requires specific status.

### *Mallacoota nananui* Myers

Fig. 3

*Mallacoota nananui* Myers, 1985a: 121, fig.95.—Myers, 1986a: 277, fig.8.—Myers, 1986b: 1389, fig.8.

**Remarks.** Myers (1985) noted that this species many be synonymous with *M. subcarinatus* (Haswell) 'form 2' and doubted the possibility that *M. nananui* and *M. subcarinatus* could be polymorphs or age-related stages of a single species. Figures of gnathopod 2 of an adult and subadult male of *M. nananui* are provided here along with the same appendage of an adult *M. subcarinata*. There seems to be sufficient morphological differences to justify maintaining the two as distinct species unless breeding experiments prove otherwise. Material from the Cook Islands has the posterior margin of the propodus of the male gnathopod 2

Table 1. List of amphipods recorded from the Cook Islands, together with their occurrence in neighbouring island archipelagos (data from Barnard, 1970; Myers, 1985, 1986a, 1986b, 1988).

| Fiji | Tonga | Niue | Cook Islands | Society Islands | Hawaii |
|---|---|---|---|---|---|
| | | | *Ronco sosa* Barnard | + | |
| | | | *Tethygeneia pacifica* (Schellenberg) | + | |
| + | | | *Gitanopsis tai* Myers | + | |
| + | | | *Paranamixis madagascariensis* Ledoyer | + | |
| | | | *Colomastix murivai* n.sp. | | |
| | + | | *Leucothoe hyhelia* Barnard | | + |
| | | | *Perioculodes aequimanus* (Kossman) | | |
| | | + | *Hyale affinis* Chevreux | + | + |
| + | | | *Parambasia nui* Myers | + | |
| + | | | *Elasmopus seticarpus* Myers | + | |
| | | + | *Elasmopus takamotus* Myers | | |
| | | | *Maera lindsae* Myers | + | |
| + | | | *Maera octodens* Sivaprakasam | + | |
| + | + | + | *Maera pacifica* Schellenberg | + | + |
| + | + | | *Maera serrata* Schellenberg | + | + |
| + | | | *Mallacoota insignis* (Chevreux) | | |
| + | + | + | *Mallacoota nananui* Myers | | |
| + | | + | *Mallacoota subcarinata* (Haswell) | | |
| + | + | | *Parelasmopus suensis* (Haswell) | + | |
| + | | + | *Amphithoe ramondi* Audouin | + | |
| + | + | | *Cymadusa brevidactyla* (Chevreux) | + | |
| + | + | | *Cymadusa pilipes* (Ledoyer) | + | |
| | | | *Pleonexes auriculata* Rabindranath | + | |
| + | + | | *Paragrubia vorax* (Chevreux) | + | + |
| + | | | *Gammaropsis setifera* (Schellenberg) | + | |
| | | | *Jassa socia* Myers | + | |
| | + | | *Bemlos dentischium* (Myers) | + | |
| + | | | *Globosolembos ovatus* Myers | + | |
| + | | + | *Podocerus hanapepe* Barnard | | + |
| + | | | *Podocerus talegus* Barnard | | + |

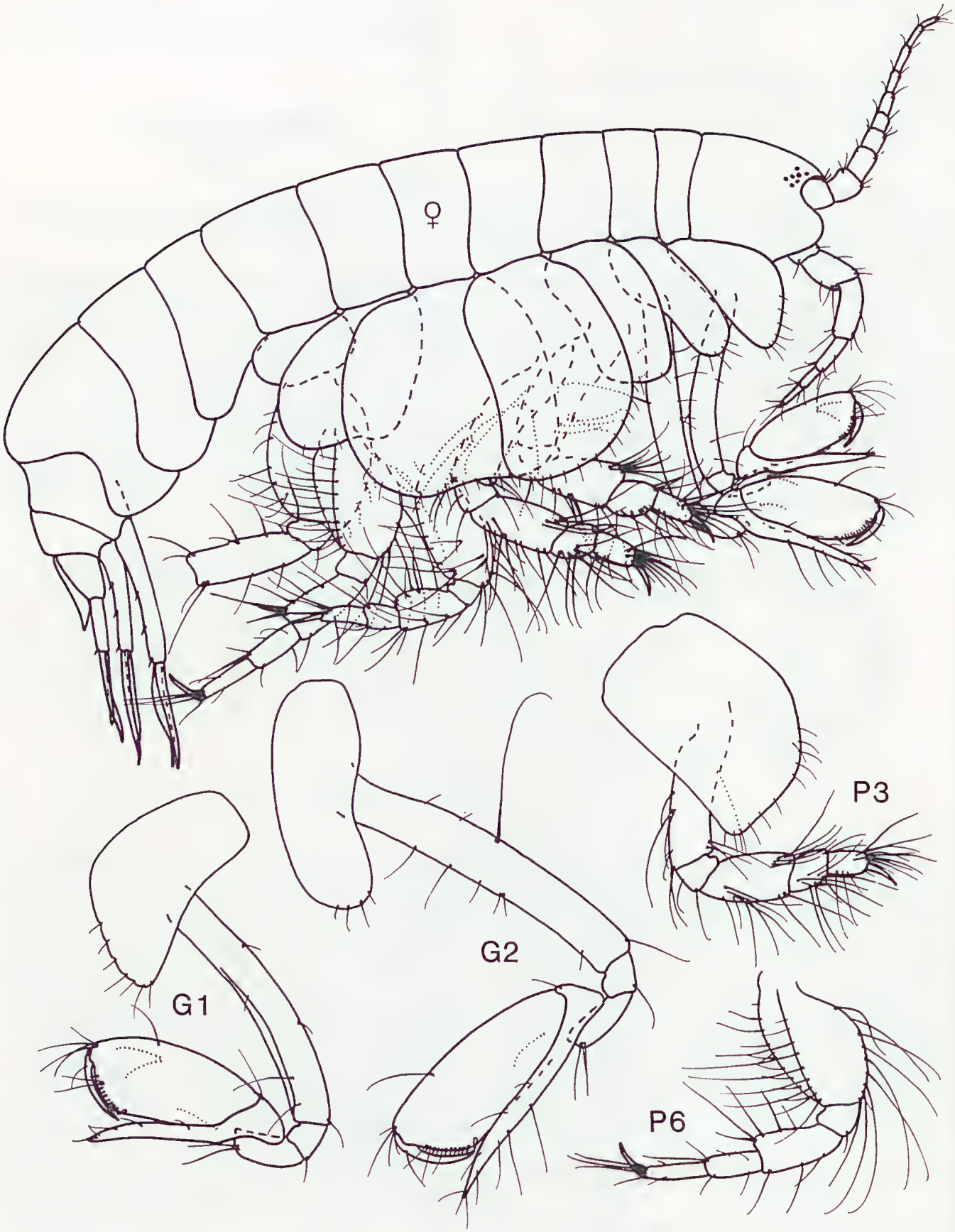


**Fig.2.** *Perioculodes aequimanus* (Kossman). Female, 2.5 mm, Rarotonga.

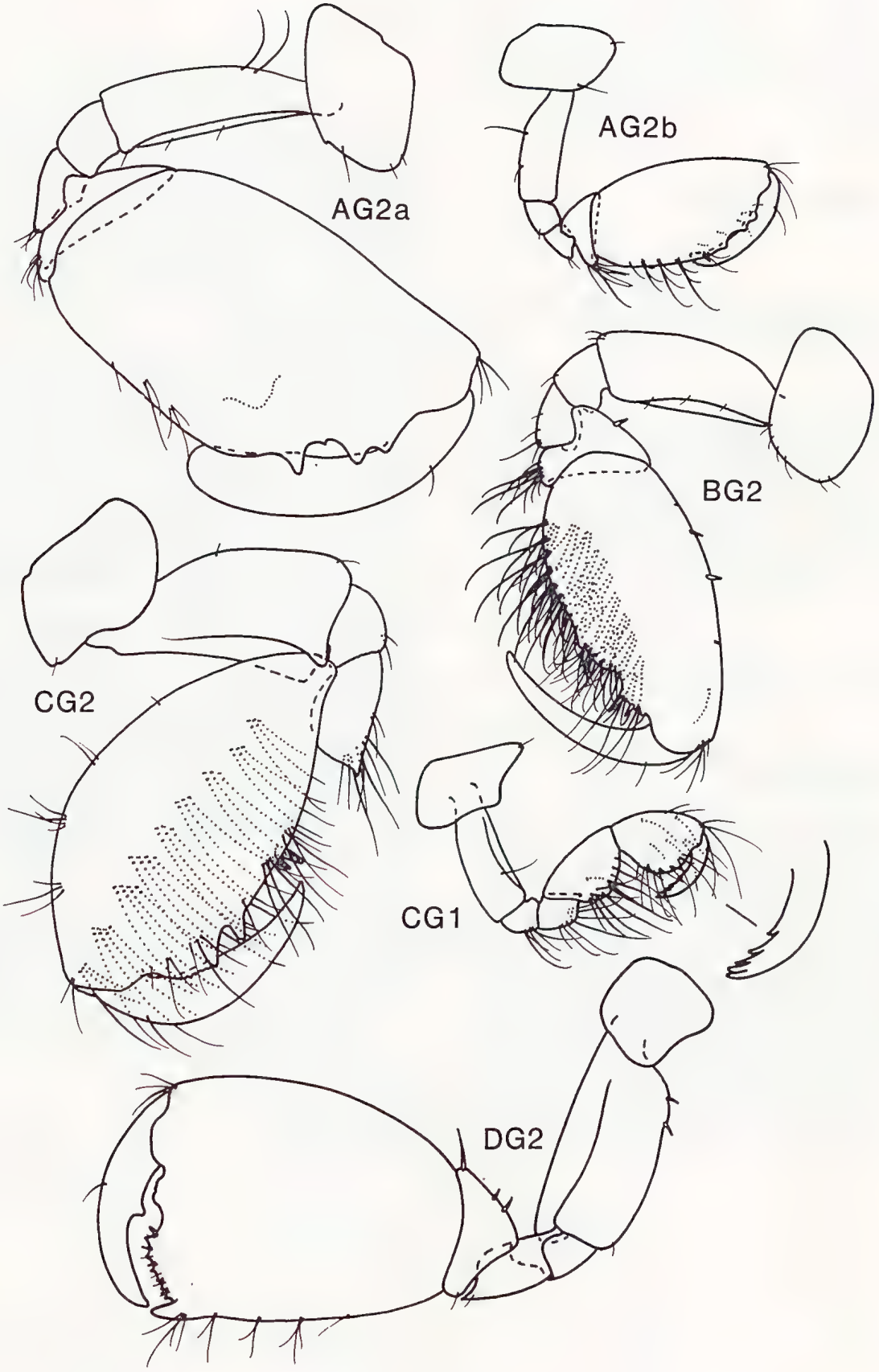


**Fig.3. A.** *Mallacoota nananui* Myers. a: male, 6.0 mm, Rarotonga; b: male, 3.7 mm, Rarotonga. **B.** *Mallacoota subcarinata* (Haswell). Male, 4.5 mm, Rarotonga. **C.** *Podocerus talegus talegus* Barnard. Male, Rarotonga. **D.** *Maera serrata* Schellenberg. Male, Rarotonga.

straight not sinuous and in this respect resembles *M. latidactyla* Ledoyer. The possibility that *M. nananui* is synonymous with *M. latidactyla* cannot be entirely discounted, but other differences outlined by Myers (1986a) suggest it is sensible to maintain *M. nananui* as distinct for the present.

### *Maera serrata* Schellenberg

Fig. 3

*Maera inaequipes serrata* Schellenberg, 1938: 41, fig.18.
*Maera serrata*.—Myers, 1985: 117, fig.92 (for full synonymy see Myers, 1985).

**Remarks.** As pointed out by Berents (1983), the palm of gnathopod 2 in *M. serrata* may show considerable variation. Present material has a much more pronounced dactylar acclivity than in Fijian material (Myers, 1985) but the opposing palmar sinus is shallow and rounded like specimens from Fiji and unlike material from Queensland (Berents, 1983). The male gnathopod 2 is figured here for future comparison with other materials.

### *Podocerus talegus talegus* Barnard

Fig. 3

*Podocerus talegus* Barnard, 1965: 544, fig.35.

**Remarks.** Present material most clearly resembles the nominate subspecies in the rather bulbous propodus of gnathopod 1 and in bearing spines on the posterior margin of the propodus of the male gnathopod 2 (a single spine figured though not described in the nominate subspecies).

The subspecies *P. talegus lawai* Barnard (1970) has a more slender gnathopod 1 propodus and lacks spines on the posterior margin of the male gnathopod 2 propodus. In the strongly toothed dactylus of gnathopod 1 present material resembles both *P. talegus lawai* and *P. talegus levuensis* Myers (1985). It differs from the latter subspecies, however, in lacking a medial tooth on the male gnathopod propodus which in *P. talegus levuensis* replaces the marginal spines.

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## Appendix 1

Station data.

Stn 1. Rarotonga, 2.5 km south of Aorangi Village, south-west coast, 21°15.1'S 159°43.9'W, 12 Nov. 1986, *Turbinaria* from reef crest.

Stn 2. Rarotonga, same locality and date, coral rubble from reef crest.

Stn 3. Rarotonga, same locality and date, *Sargassum* from reef crest.

Stn 4. Rarotonga, same locality and date, arborescent alga in lagoon.

Stn 5. Rarotonga, same locality and date, *Padina* in lagoon.

Stn 6. Rarotonga, near airport, north-west coast, 21°12.1'S 159°49.4'W, 14 Nov. 1986, *Padina* in lagoon.

Stn 7. Rarotonga, same locality and date, *Sargassum* in lagoon.

Stn 8. Rarotonga, same locality and date, *Turbinaria* in lagoon.

Stn 9. Rarotonga, 1.5 km north of Matavera, north-east coast, 21°12.4'S 159°44.5'W, 15 Nov. 1986, *Sargassum* from wave-planated terrace.

Stn 10. Rarotonga, 1 km north of Muri, 21°14.7'S 159°43.9'W, 15 Nov. 1986, coral rubble from sheltered lagoon inside motus.

Stn 11. Rarotonga, same locality and date, *Amphiroa* from sheltered lagoon inside motus.

Stn 12. Rarotonga, same locality and date, *Halimeda* from sheltered lagoon inside motus.

Stn 13. Rarotonga, near Rarotongan Hotel, 21°15.1'S 159°48.4'W, 1 Aug. 1982, rubble and algae from back of barrier reef to 1.25 km, C.A. Child, USNM.

Stn 14. Rarotonga, same locality, 2 Aug. 1982, scrapings form sand flats with coral heads and brown algae to 1.25 km, C.A. Child, USNM.

Stn 15. Mangaia, Onekoa village landing, 21°54.3'S 157°58'W, 3 Aug. 1982, calcareous algae from tidal flats, less than 1 m, C.A. Child, USNM.

## Appendix 2

Annotated list of species recorded from the Cook Islands.

| Family | Species | Males | Females | Immature | Stn No. |
|---|---|---|---|---|---|
| EUSIRIDAE | *Ronco sosa* Barnard, 1965 | 1 | | | 3 |
| | *Tethygeneia pacifica* (Schellenberg, 1938) | 1 | | | 11 |
| AMPHILOCHIDAE | *Gitanopsis tai* Myers, 1985 | 1 | 1 | | 2 |
| ANAMIXIDAE | *Paranamixis madagascariensis* Ledoyer, 1982 — Hyperadult "*Paranamixis*" | 2 | | | 1 |
| | | 1 | | | 12 |
| | "*Leucothoides*" | | 2 | | 1 |
| | | | 1 | | 13 |
| COLOMASTIGIDAE | *Colomastix murivai* n.sp. (7 slides) | | 1 | | 2 |
| LEUCOTHOIDAE | *Leucothoe hyhelia* Barnard | 1 | 2 | | 1 |
| | | | 1 | | 2 |
| | | | 1 | | 8 |

Appendix 2. cont'd.

| Family | Species | Males | Females | Immature | Stn No. |
|---|---|---|---|---|---|
| OEDICEROTIDAE | *Perioculodes aequimanus* (Kossman, 1880) | | 1 | | 5 |
| HYALIDAE | *Hyale affinis* Chevreux, 1907 | 10 | 25 | 1 | 1 |
| | | | 1 | | 2 |
| LYSIANASSIDAE | *Parambasia nui* Myers, 1985 | | 2 | | 10 |
| | | | 1 | | 11 |
| | | 3 | 3 | | 13 |
| | | 1 | 2 | | 14 |
| MELITIDAE | *Elasmopus seticarpus* Myers, 1985 | 1 | 2 | | 3 |
| | | 1 | 1 | 1 | 5 |
| | | 3 | 3 | | 10 |
| | *Elasmopus takamotus* Myers, 1985 | 4 | 4 | 4 | 15 |
| | *Maera lindsae* Myers, 1989 | | 1 | | 10 |
| | *Maera octodens* | 1 | 4 | | 12 |
| | Sivaprakasam, 1968 | 2 | 2 | | 13 |
| | | | 1 | | 14 |
| | *Maera pacifica* | 1 | 6 | 3 | 2 |
| | Schellenberg, 1938 | 1 | 3 | | 5 |
| | | 2 | 1 | | 11 |
| | | | 2 | 4 | 15 |
| | *Maera serrata* Schellenberg, 1938 | 3 | 5 | 2 | 1 |
| | | 1 | 1 | 1 | 6 |
| | | | 1 | | 10 |
| | | 7 | 9 | | 11 |
| | | 8 | 13 | | 12 |
| | | 1 | 1 | | 14 |
| | *Mallacoota insignis* (Chevreux, 1901) | 1 | 1 | | 3 |
| | *Mallacoota subcarinata* (Haswell, 1880) | 1 | 9 | | 1 |
| | *Mallacoota nananui* Myers, 1985 | 1 | | | 1 |
| | | 1 | 1 | | 3 |
| | | 4 | 7 | 10 | 4 |
| | | 10 | 18 | | 5 |
| | | 1 | 4 | | 6 |
| | | 3 | 13 | | 10 |
| | | 12 | 12 | | 11 |
| | | 9 | 11 | | 12 |
| | | 1 | 3 | | 13 |
| | | 1 | 6 | | 14 |
| | *Parelasmopus suensis* | | 1 | | 5 |
| | (Haswell, 1880) | 4 | 3 | | 12 |
| | | | 1 | | 13 |
| AMPITHOIDAE | *Amphithoe ramondi* | 1 | | | 6 |
| | Audouin, 1826 | 1 | 3 | | 13 |
| | | | 1 | | 14 |
| | *Cymadusa brevidactyla* | | 2 | | 1 |
| | (Chevreux, 1907) | 5 | 5 | 4 | 5 |
| | | | 3 | | 6 |
| | | 1 | 2 | | 11 |
| | | | 4 | 1 | 13 |
| | *Cymadusa pilipes* (Ledoyer, 1984) | 1 | 3 | | 1 |
| | | 1 | 1 | | 3 |
| | | 1 | 8 | | 4 |
| | | 14 | 48 | | 10 |
| | | 4 | 8 | | 12 |
| | *Paragrubia vorax* Chevreux, 1901 | | 1 | | 2 |

Appendix 2. cont'd.

| Family | Species | Males | Females | Immature | Stn No. |
|---|---|---|---|---|---|
| AMPITHOIDAE (cont'd) | *Pleonexes auriculata* Rabindranath, 1972 | 17 | 28 | | 1 |
| | | | 3 | | 2 |
| | | 2 | 4 | | 3 |
| | | | 2 | | 4 |
| | | 3 | 3 | 2 | 5 |
| | | 1 | 11 | 1 | 6 |
| | | 6 | 13 | | 13 |
| ISAEIDAE | *Gammaropsis setifera* (Schellenberg, 1938) | 10 | 14 | | 1 |
| | | 2 | 1 | | 3 |
| | | 24 | 36 | 19 | 8 |
| ISCHYRODERIDAE | *Jassa lilipuna socia* Myers, 1989 | 9 | 1 | | 1 |
| | | | 1 | | 2 |
| | | 6 | 4 | | 3 |
| | | | 1 | | 4 |
| | | | 3 | | 6 |
| | | 2 | | | 10 |
| | | 3 | 2 | | 11 |
| AORIDAE | *Bemlos dentischium taparum* Myers, 1985 | 1 | 3 | | 1 |
| | | | | 1 | 2 |
| | | 1 | 1 | 4 | 4 |
| | | 1 | | | 8 |
| | | 4 | 9 | | 12 |
| | | 1 | 2 | | 13 |
| | *Globosolembos ovatus* Myers, 1985 | 2 | 5 | | 10 |
| | | 1 | 1 | | 13 |
| | | | 1 | | 14 |
| PODOCERIDAE | *Podocerus hanapepe* Barnard, 1970 | 5 | 1 | | 1 |
| | | | 1 | | 2 |
| | *Podocerus talegus lawai* Barnard, 1970 | 8 | 6 | | 1 |
| | | 1 | 2 | | 2 |
| | | 14 | 21 | 2 | 3 |
| | | 6 | 6 | | 4 |
| | | | 1 | | 6 |
| | | 2 | 6 | | 8 |
| | | 2 | | | 13 |

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# The Wandinidae, a New Indo-Pacific Family of Lysianassoid Amphipoda (Crustacea)

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Abstract. The family Wandinidae is established for *Pseudocyphocaris* Ledoyer and the new genus *Wandin*. Both genera are known only from the Indo-Pacific area. The Wandinidae is characterised by a peculiar hook-like process on the peduncle of antenna 2, a conical mouthpart bundle, coxae 1 to 3 variously reduced, coxa 4 greatly enlarged, and a 1-articulate outer ramus on uropod 3 with a subapical incision. The Wandinidae is considered to be the sister group of the amaryllidid family group. One new species of *Wandin* is described from the Great Barrier Reef, Australia and two new species of *Pseudocyphocaris* are described from north-eastern Papua New Guinea.

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Ledoyer (1986) described *Pseudocyphocaris coxalis* from Madagascar and placed it in the family Lysianassidae. J.D. Thomas recently collected two new species from Papua New Guinea which we describe here. A second closely related genus was found in collections from the Great Barrier Reef and is described here as *Wandin griffini*.

These two genera have simple first gnathopods and superficially resemble the Lysianassinae as defined by Hurley (1963). However, *Wandin* and *Pseudocyphocaris* share distinctive synapomorphies which preclude them from the subfamily Lysianassinae. They do not belong in the conicostomatid group of Lowry & Stoddart (1983) or the amaryllidid group of Lowry & Stoddart (in preparation) for similar reasons. We are therefore establishing a new family, the Wandinidae, for these genera.

## Methods

All material is lodged in the Australian Museum, Sydney (AM). Abbreviations used in the figures are as follow: A1,2 – antenna 1,2; C – coxa; E – epistome and upper lip; EP3 – epimeral plate 3; G1,2 – gnathopod 1,2; H – head; MD – mandible; MP – maxilliped; MPp – maxilliped palp; MPIP – maxilliped inner plate; MPOP – maxilliped outer plate; MX1-2 – maxilla 1,2; P3-7 – peraeopod 3-7; ST1-7 – maxilla 1 outer plate outer row spine-tooth 1-7; STA-D – maxilla 1 outer plate inner row spine-tooth A-D; T – telson; U1-3 – uropod 1-3; l – left; r – right.

Most lysianassoids have 11 spine-teeth in two rows on the outer plate of maxilla 1. To clarify comparative studies and homologies a letter and number code for each of these teeth is introduced (Fig. 8). In some taxa the outer row contains 7 spine-teeth (ST1-ST7) and the inner row

Contribution No. 52, Christensen Research Institute, Madang, Papua New Guinea. Contribution No. 300, Lizard Island Research Station, Lizard Island, Queensland, Australia.

contains 4 (STA-STD). In many taxa however, the outer plate is narrowed and the first spine-tooth of the outer row (ST1) is displaced onto the inner row. This in turn usually displaces the first spine-tooth of the inner row (STA). A more detailed report on maxilla 1 spine-teeth in lysianassoids is in preparation.

## Wandinidae n.fam.

**Type genus.** *Wandin* n.gen.

**Description.** *Head deeper than long, with a subtriangular lateral cephalic lobe.* Antenna 1, peduncle slightly elongate, articles 2 and 3 not compressed; callynophore weakly developed in female and male; calceoli not present in female or male. *Antenna 2: laterodistal margin of peduncular article 3 produced into a large hook-like process;* flagellum not elongate in male, calceoli not present in female or male. *Mouthpart bundle conical.* Mandible, left lacinia mobilis a simple spine or peg; accessory spine row well developed, more than 3 accessory spines; molar absent; palp attached extremely proximally. Maxilla 1, inner plate narrow, with 1 simple apical seta; outer plate with 9–11 spine-teeth, ST1 displaced onto inner row; outer row with 5–6 spine-teeth, left and right ST7 asymmetrical; inner row with 4–5 spine-teeth; palp large, 1-articulate, not spinose apically. Maxilliped, inner plate densely covered in setae, oblique plumose setal row vestigial or absent, apical nodular spines vestigial or absent; outer plate without apical setae, apical spines, marginal spines or submarginal setae; palp article 4 vestigial or fused to article 3. *Coxae 1 to 3 variously reduced, coxa 4 greatly enlarged with well-developed posteroventral lobe, coxa 5 shallow, much broader than deep, not lobate.* Gnathopod 1 simple, propodus with strongly serrate posterior margin bearing a large midmedial spine. Gnathopod 2 subchelate, palm minutely developed, bordered by at least one strong spine. Peraeopods 3 and 4: male merus and carpus without plumose setae. Peraeopods 5 and 6: basis linear. Peraeopod 7: basis greatly expanded. Gills present from gnathopod 2 to peraeopod 6 or 7, not pleated. Oostegites from peraeopods 2 to 5. Uropods well developed. Uropod 2: inner ramus incised or not. *Uropod 3: peduncle with well-developed lateral flange, rami lanceolate, outer ramus 1-articulate, with subapical incision.* Telson entire, longer than broad.

**Remarks.** The Wandinidae are most similar to lysianassoid family groups with simple first gnathopods. They do not belong to the Lysianassinae as defined by Hurley (1963) because the mouthparts are conical, the accessory spine row on the mandible is very well developed, the palp of maxilla 1 is 1-articulate, the simple gnathopod 1 has a strongly serrate posterior margin, coxae 1–3 are variously reduced, coxa 5 is nonlobate and the third uropods are apically incised.

Wandinids differ from the conicostomatid group of Lowry & Stoddart (1983) because the accessory spine row on the mandible is very well developed, the arrangement and shape of spine-teeth on maxilla 1 is different, the posterior margin of gnathopod 1 is strongly serrate, coxae 1–3 are variously reduced and the third uropods are apically incised.

We consider wandinids and amaryllidids (Lowry & Stoddart, in preparation) to be sister groups. Both families share a fused epitome/upper lip, an elongate accessory spine row on the mandible, a peculiar rudimentary maxillipedal palp article 4, and almost identical first gnathopods with a posteriorly serrate margin on the propodus. Wandinids differ from the amaryllidid family group in having a short head which lacks a lateral cephalic cheek notch; no mandibular molar; a well-developed palp on maxilla 1; different spine-teeth on the outer plate of maxilla 1; a nonlobate coxa 5; apically incised third uropods; and an entire telson.

Wandinids are presumed to be commensals. There is some evidence that they are associated with colonial tunicates. They are currently known only from shallow coastal waters of Madagascar, Papua New Guinea and tropical Australia.

## Key to the Wandinidae

1. Coxae 1–3 extremely reduced; anterior margin of coxa 4 convex; maxilla 1 with 11 spine-teeth ..... 2

—— Coxa 1 extremely reduced, coxae 2–3 large; coxa 4 with straight anterior margin; maxilla 1 with 9 spine-teeth ..... *Wandin griffini*

2. Coxa 6 with posterior lobe slightly produced or not produced ventrally; maxillipedal palp 3-articulate ..... 3

—— Coxa 6 with posterior lobe greatly produced ventrally; maxillipedal palp 4-articulate ..... *Pseudocyphocaris lobata*

3. Coxa 6 with posterior lobe not produced ventrally ..... *Pseudocyphocaris coxalis*

—— Coxa 6 with posterior lobe slightly produced ventrally ..... *Pseudocyphocaris gosema*

## *Wandin* n.gen.

**Type species.** *Wandin griffini* n.sp.

**Diagnosis.** *Mandible:* lacinia mobilis a narrow spine. *Maxilla 1:* outer plate with 9 spine-teeth. *Coxa 1:* extremely reduced, coxae 2–3 well developed. *Coxa 4:* greatly expanded anteriorly and posteriorly, anterior margin straight. *Uropod 2:* inner ramus not incised.

**Remarks.** *Wandin* is currently a monotypic genus known only from tropical Australia. *Pseudocyphocaris* and *Wandin* are very similar genera. The main differences between them are the reduced number of spine-teeth on the outer plate of maxilla 1 in *Wandin*, the reduction of coxae 2 and 3 in *Pseudocyphocaris* and the shape of the anterior margin of coxa 4.

**Etymology.** "Wandin" is taken from the Guugu-Yimidhirr language of people in the Lizard Island area. It is the name for a bark shield used to protect the legs from spears and alludes to the large fourth coxal shield which characterises the family.

## *Wandin griffini* n.sp.

Figs 1–3, 8D

**Type material.** HOLOTYPE, sex indeterminate, 2.0 mm, AM P39209; PARATYPE, AM P39210; south end of reef north of Ferguson Reef, Great Barrier Reef, Australia, 12°20'S 143°51'E, rubble washings from coral slope, 10–12 m, I. Loch, 8 Dec. 1982, QLD-88; 4 PARATYPES, AM P39211, between Lizard Island and Carter Reef, Great Barrier Reef, 14°35'S 145°35'E, algae, 32-38 m, epibenthic sled, J.M. Leis, 26 Nov. 1981, JML 81/26-11-4; 7 PARATYPES, AM P39212, Mrs Watsons Bay, Lizard Island, Great Barrier Reef, 14°40'S 145°28'E, formalin wash of rubble from patch reef, 1–7 m, J.D. Thomas, 25 Jan. 1989, JDT/LIZ-7; 4 PARATYPES, AM P39213, Mermaid Beach, Lizard Island, Great Barrier Reef, 14°40'S 145°28'E, formalin wash of rubble, 1–2 m, J.D. Thomas, 26 Jan. 1989, JDT/LIZ-8; 7 PARATYPES, AM P39214, North Point, Lizard Island, Great Barrier Reef, 14°40'S 145°28'E, coral rubble, 12 m, J.D. Thomas, 28 Jan. 1989, JDT/LIZ-13.

**Diagnosis.** As for genus.

**Fig.1.** *Wandin griffini* n.gen., n.sp., paratype, AM P39212, Lizard Island, Great Barrier Reef, Australia.

**Description.** Based on holotype, 2.0 mm, ovigerous paratype female, 2.5 mm, AM P39212 and paratype male, 2.1 mm, AM P39214. *Colour in life:* translucent white with deep red colouring on peduncle of antenna 1, anterior portion of head, middle of body (in form of a ventrally tapered saddle on posterior half of peraeonite 4, anterior half of peraeonite 5 and part of coxa 4) and dorsum of pleonite 1. Eye black. *Head:* deeper than long,lateral cephalic lobe subtriangular; rostrum absent; eyes round, not enlarged in reproductive male. *Antenna 1:* short, 0.2 times as long as body, slightly shorter than antenna 2; peduncular article 1 of medium length, 1.5 times as long as deep; without midmedial tooth; accessory flagellum 2-articulate, not forming cap; callynophore, reduced 1-field in female and male; flagellum short, 6-articulate; calceoli absent. *Antenna 2:* peduncle without brush setae, peduncular article 3 with a large distal hook on lateral face, peduncular articles 4 and 5 not swollen; flagellum not elongate in reproductive male; calceoli absent.

*Mouthpart bundle:* conical. *Epistome* and *upper lip:* fused, margin straight in profile. *Mandible:* incisors

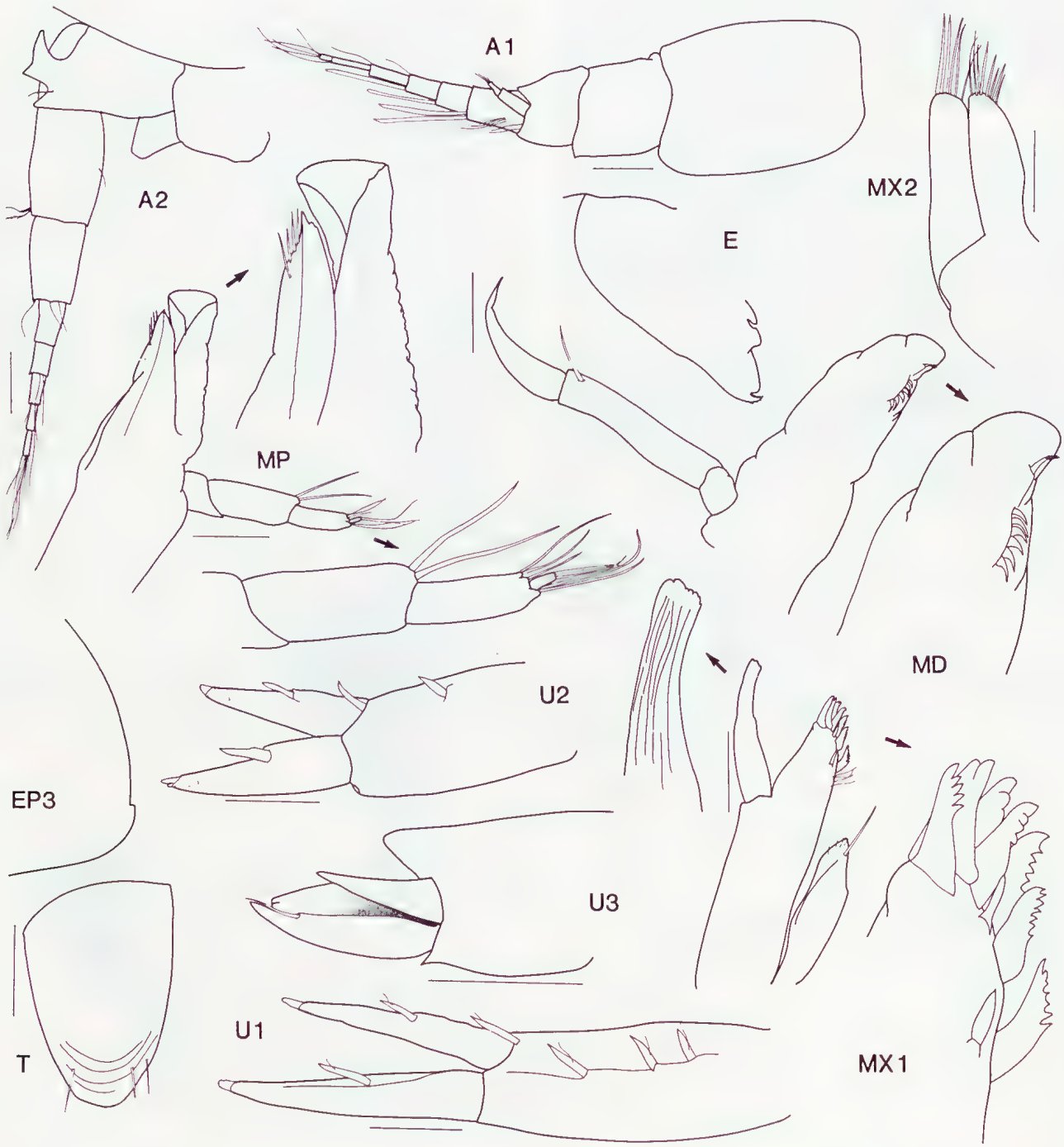


**Fig.2.** *Wandin griffini* n.gen., n.sp., holotype, 2.0 mm, AM P39209, Ferguson Reef, Great Barrier Reef, Australia. Scales represent 0.1 mm.

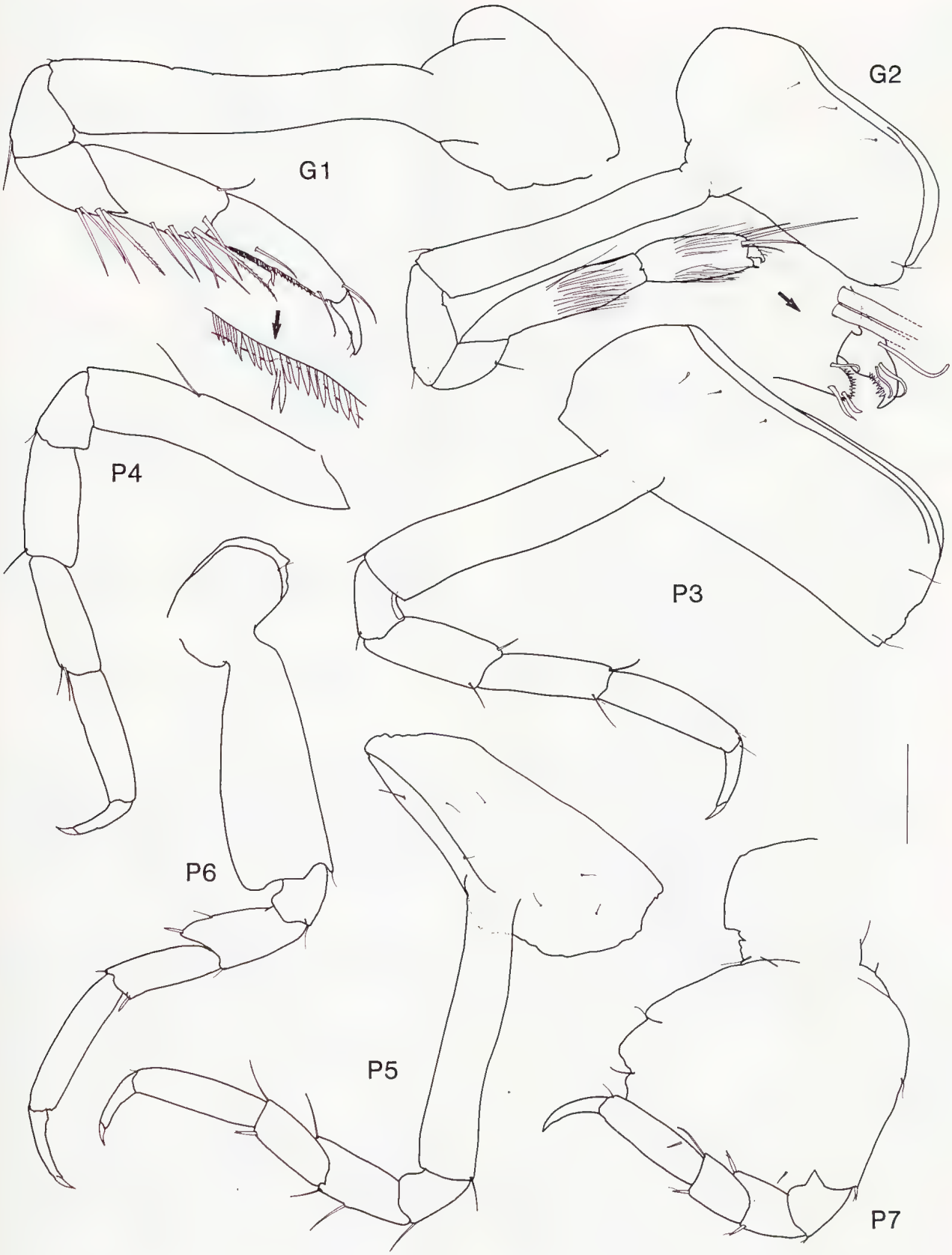


**Fig.3.** *Wandin griffini* n.gen., n.sp., holotype, 2.0 mm, AM P39209, Ferguson Reef, Great Barrier Reef, Australia. Scales represent 0.1 mm.

narrow, symmetrical, both with slightly convex margins; left lacinia mobilis a simple spine; accessory spine row, left and right each with 6 small stout spines; molar absent; mandibular palp attached extremely proximally; article 1 short, about as long as broad; article 2 elongate, slender, with 1 distomedial seta; article 3 weakly falcate, setae absent. *Maxilla 1:* inner plate narrow with 1 apical simple seta; outer plate narrow, with 9 spine-teeth in 2 rows, outer row (probably ST2 absent) with ST1, ST3 to ST7, large, weakly to multicuspidate, left ST7 with elongate inner margin, 6-cuspidate distal margin, right ST7 with short inner margin, 8-cuspidate distal margin, both displaced from ST6; inner row with STA large, 4-cuspidate distally, STB small, simple, STC absent, STD small, simple; palp large, 1-articulate, with minutely serrate apical margin. *Maxilla 2:* inner and outer plates subequal in length and breadth. *Maxilliped:* inner plate long, slender, without apical nodular spines, oblique setal row vestigial, with 4 simple setae; outer plate large, apical setae, apical spines, medial spines and submarginal setae all absent; palp small, 4-articulate, dactylus vestigial, unguis absent, 2 terminal setae.

*Gnathopod 1:* simple; coxa extremely reduced; carpus subrectangular, 2.4 times as long as deep, posterior margin not lobate, subequal in length to propodus; propodus subrectangular, 3.0 times as long as deep, tapering distally; posterior margin serrate, straight, with 1 midmedial spine; dactylus simple, without subterminal tooth. *Gnathopod 2:* minutely subchelate; coxa large, about two thirds length of coxa 3; carpus linear, elongate, 4.6 times as long as deep; propodus subrectangular, 2.6 times as long as deep; palm obtuse, with convex margin; posterodistal corner with 1 medial spine.

*Peraeopods 3–7:* with short, slender dactyli. *Peraeopod 3:* simple; coxa large. *Peraeopod 4:* simple; coxa extremely large, produced anteriorly and posteriorly, anterior margin straight with rounded anteroventral corner, posterior lobe produced as far as coxa 6. *Peraeopod 5:* coxa shallow, much broader than deep, tapering posteriorly, not lobate; basis linear with posterior margin straight. *Peraeopod 6:* coxa small, not lobate posteriorly, basis linear, broader than basis of peraeopod 5, slightly expanded posterodistally. *Peraeopod 7:* basis extremely expanded posteriorly, subtriangular posterior margin slightly crenulate, with a long, slightly rounded posteroventral margin; merus slender, only slightly expanded posteriorly. *Gills:* from gnathopod 2 to peraeopod 6, not pleated.

*Epimeron 3:* with a rounded posteroventral corner and a high tiny notch on posterior margin. *Uropod 1:* outer ramus slightly longer than inner. *Uropod 2:* peduncle elongate; outer ramus slightly longer than inner, not incised; each ramus with simple spine. *Uropod 3:* peduncle short, 1.2 times as long as deep, with dorsolateral flange; rami lanceolate; inner ramus 0.67 times as long as outer ramus; outer ramus 1-articulate, broad with a subapical incision; plumose setae absent in female and male. *Telson:* 1.5 times as long as broad, entire, without dorsal spines, distal margins rounded, with 2 pairs of subapical simple setae.

**Remarks.** *Wandin griffini* is presumed to be a commensal because of the structure of its mouthparts. It is currently known only from the northern part of the Great Barrier Reef in depths of 1 to 38 m.

**Etymology.** We are especially pleased to name this species after Dr D.J.G. Griffin in recognition of his significant contribution to Indo-Pacific carcinology.

### *Pseudocyphocaris* Ledoyer

*Pseudocyphocaris* Ledoyer, 1986: 802.

**Type species.** *Pseudocyphocaris coxalis* Ledoyer, 1986, by original designation.

**Diagnosis.** *Mandible:* lacinia mobilis a small peg. *Maxilla 1:* outer plate with 11 spine-teeth. *Coxae 1–3:* extremely reduced. *Coxa 4:* greatly expanded anteriorly and posteriorly, anterior margin convex. *Uropod 2:* inner ramus incised.

**Remarks.** *Pseudocyphocaris* is known from Madagascar and Papua New Guinea. For comments on similarities to *Wandin* see remarks for that genus.

### *Pseudocyphocaris gosema* n.sp.

Figs4–5,8C

**Type material.** HOLOTYPE, female, 2.5 mm, AM P39215, Paddock Reef, off Gosem Island, near Madang, Papua New Guinea, approx. 5°12'S 145°47'E, in association with *Didemnum molle*, formalin wash of coral rubble from patch reef, 3 m, J.D. Thomas, 7 Jan. 1989, JDT/PNG-1.

**Diagnosis.** *Colour:* body pale orange mottled with darker orange spots; antenna 1 peduncle light red with dark red stripe on article 1; peraeonite 4 with a dark red tapering stripe. Eye pale orange. *Maxilla 2:* inner plate broader than outer. *Maxillipedal palp:* 3-articulate, propodus and dactylus fused. *Coxa 4:* posterior margin reaching to coxa 6. *Peraeopod 6:* coxa slightly lobate posteriorly.

**Description.** Holotype female, 2.5 mm; male not known. *Colour one week after preservation:* body pale orange mottled with darker orange spots; antenna 1 peduncle light red with dark red stripe on article 1; peraeonite 4 with a dark red tapering stripe. Eye pale orange. *Head:* deeper than long, lateral cephalic lobe subtriangular; rostrum absent; eyes oval. *Antenna 1:* short, 0.2 times as long as body, slightly shorter than antenna 2; peduncular article 1 of medium length, 1.5 times as long as deep; without midmedial tooth; accessory flagellum

**Fig.4.** *Pseudocyphocaris gosema* n.sp., holotype, female, 2.5 mm, AM P39215, Gosem Island, Papua New Guinea. Scales represent 0.1 mm.

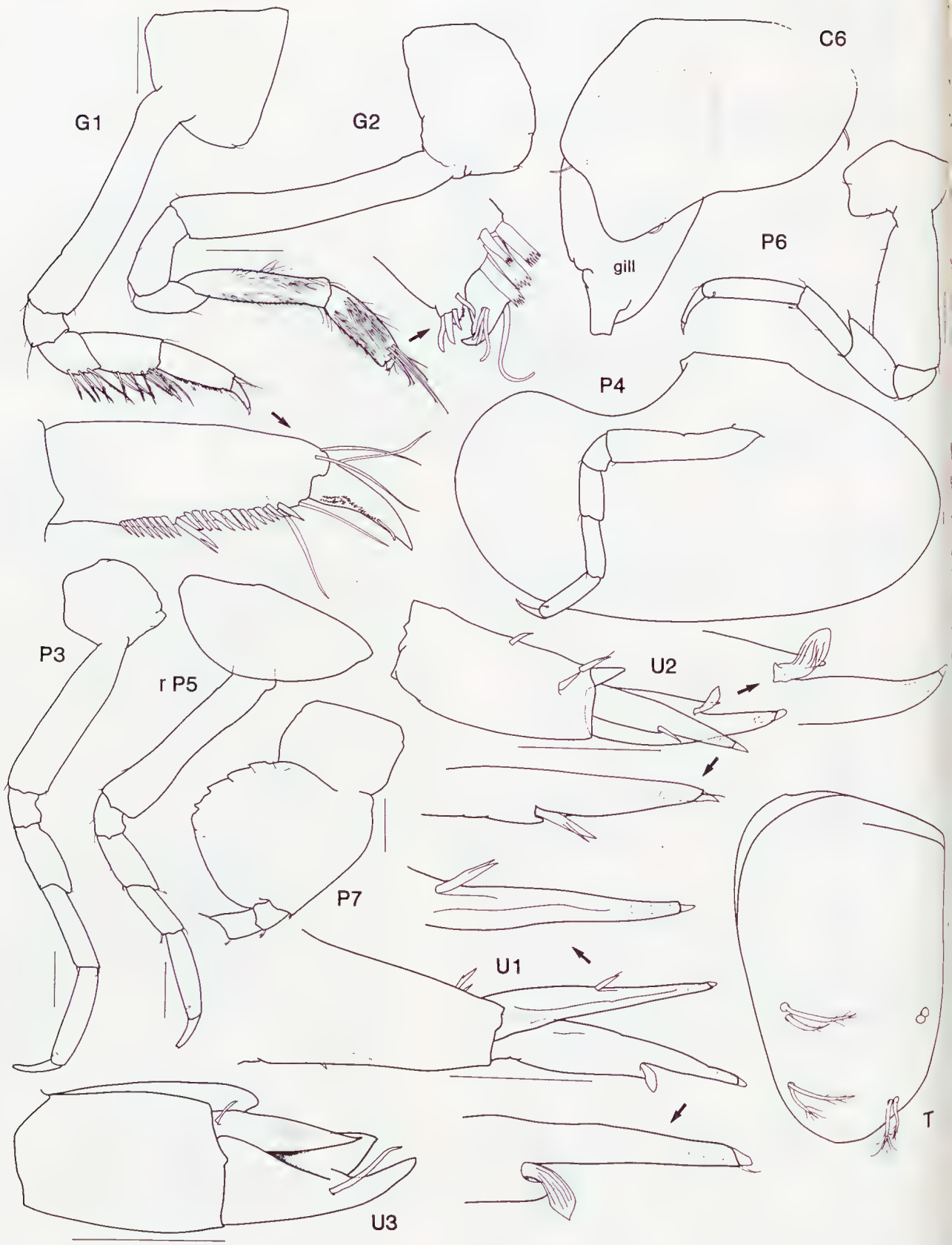


**Fig.5.** *Pseudocyphocaris gosema* n.sp., holotype, female, 2.5 mm, AM P39215, Gosem Island, Papua New Guinea. Scales represent 0.1 mm.

1-articulate, not forming cap; callynophore, reduced 1-field; flagellum short, 5-articulate; calceoli absent. *Antenna 2:* peduncle without brush setae, peduncular article 3 with a large distal hook on lateral face, peduncular articles 4 and 5 not swollen, calceoli absent.

*Mouthpart bundle:* conical. *Epistome* and *upper lip:* fused, margin straight in profile. *Mandible*: incisors narrow, symmetrical, both with slightly convex margins; left lacinia mobilis a cuspidate peg; accessory spine row, left and right each with 16 small stout spines; molar absent; mandibular palp attached extremely proximally; article 1 elongate, nearly twice as long as broad; article 2 elongate, slender, with 1 large distomedial seta; article 3 weakly falcate, setae absent. *Maxilla 1:* inner plate not known; outer plate narrow, with 11 spine-teeth in 2 rows, outer row with ST1 to ST7, large, weakly to multicuspidate, left ST7 with elongate inner margin, 5-cuspidate distal margin, right ST7 with short inner margin, 7-cuspidate distal margin, both displaced from ST6; inner row with STA displaced from STB, large, simple, STB–STD small, simple; palp large, 1-articulate, with bifurcate apical margin. *Maxilla 2:* inner plate broader than outer, plates subequal in length. *Maxilliped:* inner plate long, slender, apical nodular spines and oblique setal row absent; outer plate large, apical setae, apical spines, medial spines and submarginal setae all absent; palp small, 3-articulate, propodus and dactylus fused, 4 terminal and 2 subterminal setae.

*Gnathopod 1:* simple; coxa extremely reduced; carpus subrectangular, 2.1 times as long as deep, subequal in length to propodus; propodus subrectangular, 2.75 times as long as deep, margins tapering distally; posterior margin serrate, straight, with 1 midmedial spine; dactylus simple, without subterminal tooth. *Gnathopod 2:* minutely subchelate; coxa extremely reduced, subequal in size to coxa 3; carpus elongate, subrectangular, 4.6 times as long as deep; propodus elongate, subrectangular, 2.6 times as long as deep, not broadly lobate; palm transverse, with convex margin; posterodistal corner with 2 medial spines.

*Peraeopods 3–7:* with short, slender dactyli. *Peraeopod 3:* simple; coxa extremely reduced. *Peraeopod 4:* simple; coxa extremely large, produced anteriorly and posteriorly, anterior margin convex, posterior lobe produced as far as coxa 7. *Peraeopod 5:* coxa shallow, much broader than deep, tapering posteriorly, not lobate; basis linear with posterior margin straight. *Peraeopod 6:* coxa small, slightly lobate posteriorly; basis linear, broader than basis of peraeopod 5, slightly expanded posterodistally. *Peraeopod 7:* basis extremely expanded posteriorly, subtriangular posterior margin crenulate, with a long slightly rounded posteroventral margin; merus slender, only slightly expanded posteriorly. *Oostegites:* from gnathopod 2 to peraeopod 5. *Gills:* from gnathopod 2 to peraeopod 6, not pleated.

*Epimeron 3:* with a small tooth on posteroventral corner. *Uropod 1:* outer ramus slightly longer than inner with large striated spine inserted in deep cleft; inner ramus with simple spine in shallow cleft. *Uropod 2:* peduncle elongate; outer ramus slightly longer than inner with large striated spine inserted in deep cleft; inner ramus with simple spine in shallow cleft. *Uropod 3:* peduncle short, 1.4 times as long as deep, with lateral flange; rami lanceolate; inner ramus 0.72 times as long as outer ramus; outer ramus 1-articulate, broad with a subapical incision; plumose setae absent. *Telson:* 1.5 times as long as broad, entire, without dorsal spines, distal margin rounded, with 2 pairs of subapical penicillate setae.

**Remarks.** *Pseudocyphocaris gosema* is related to *P. coxalis* by its 3-articulate maxillipedal palp. It is similar to *P. lobata* in coxa 6 which is slightly lobate posteroventrally.

**Etymology.** The species takes its name from the type locality, Gosem Island.

### *Pseudocyphocaris lobata* n.sp.

Figs6–8B

**Type material.** HOLOTYPE, sex not known, 2.2 mm, AM P39216, Paddock Reef, off Gosem Island, near Madang, Papua New Guinea, approx. 5°12'S 145°47'E, in association with *Didemnum molle*, formalin wash of coral rubble from patch reef, 3 m, J.D. Thomas, 7 Jan. 1989, JDT/PNG-1.

**Diagnosis.** *Colour:* translucent green with deep red colouring on peduncle of antenna 1, anterior portion of head, middle of body (in form of a ventrally tapered saddle on posterior half of peraeonite 4, anterior half of peraeonite 5 and part of coxa 4)and dorsum of pleonite 1. *Maxilla 2:* inner and outer plates subequal in breadth. *Maxillipedal palp:* 4-articulate, article 4 vestigial. *Coxa 4:* posterior margin reaching to coxa 6. *Peraeopod 6:* coxa greatly lobate posteriorly.

**Description.** Holotype, 2.2 mm. *Colour in life:* translucent green with deep red colouring on peduncle of antenna 1, anterior portion of head, middle of body (in form of a ventrally tapered saddle on posterior half of peraeonite 4, anterior half of peraeonite 5 and part of coxa 4) and dorsum of pleonite 1. Eye black. *Head:* deeper than long, lateral cephalic lobe subtriangular; rostrum absent; eyes oval. *Antenna 1:* short, 0.2 times as long as body, slightly shorter than antenna 2; peduncular article 1 of medium length, 1.5 times as long as deep; without midmedial tooth; accessory flagellum 1-articulate, not forming cap; callynophore, reduced 1-field; flagellum short, 5-articulate; calceoli absent. *Antenna 2:* peduncle without brush setae, peduncular article 3 with a large distal hook on lateral face, peduncular articles 4 and 5 not swollen; calceoli absent.

*Mouthpart bundle:* conical. *Epistome and upper lip:* fused, margin straight in profile. *Mandible:* incisors narrow, symmetrical, both with slightly convex margins; left lacinia mobilis a cuspidate peg; accessory spine row, left and right each with 13 small stout spines; molar absent; mandibular palp attached extremely proximally, article 1 elongate,

nearly twice as long as broad, article 2 elongate, slender, with 1 large distomedial seta; article 3 weakly falcate, setae absent. *Maxilla 1:* inner plate not known; outer plate narrow, with 11 spine-teeth in 2 rows, outer row with ST1 to ST7, large, weakly to multicuspidate, left ST7 with elongate inner margin, 6-cuspidate distal margin, right ST7 with short inner margin, 10-cuspidate distal margin, both displaced from ST6; STA displaced from STB, large, simple, STB–STD small, simple, STD displaced from STC; palp large, 1-articulate, with bifurcate apical margin. *Maxilla 2:* inner and outer plates subequal in length and breadth. *Maxilliped:* inner plate long, slender, apical nodular spines and oblique setal row absent; outer plate large, apical setae, apical spines, medial spines and submarginal setae all absent; palp small, 4-articulate, dactylus vestigial with 2 terminal setae.

*Gnathopod 1:* simple; coxa extremely reduced; carpus subrectangular, 2.4 times as long as deep, subequal in

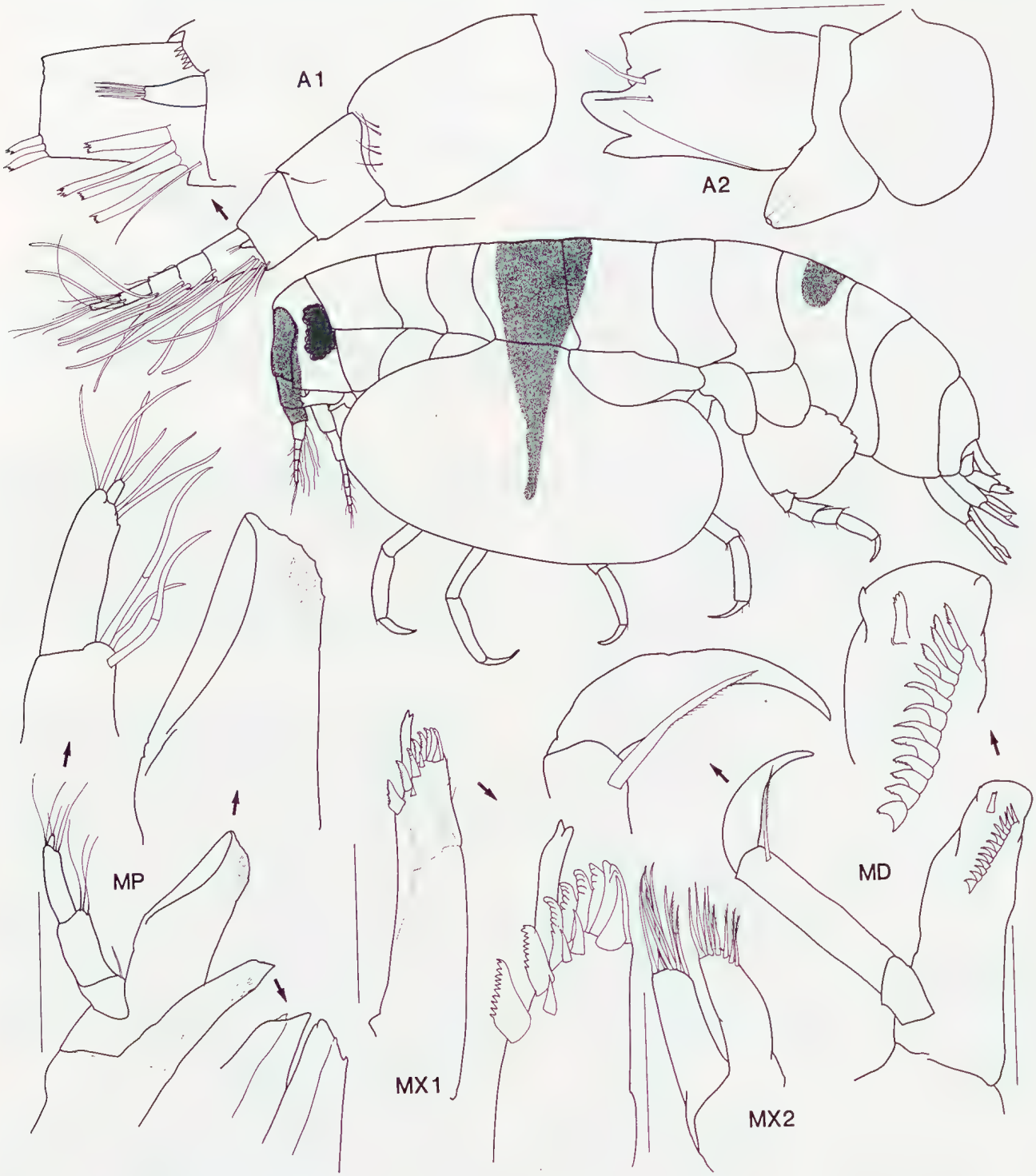


**Fig.6.** *Pseudocyphocaris lobata* n.sp., holotype, 2.2 mm, AM P39216, Gosem Island, Papua New Guinea. Scales represent 0.1 mm.

length to propodus; propodus subrectangular, 2.8 times as long as deep, tapering distally; posterior margin serrate, straight, with 1 midmedial spine; dactylus simple, without subterminal tooth. *Gnathopod 2:* minutely subchelate; coxa extremely reduced, subequal in size to coxa 3; carpus subrectangular, 5.2 times as long as deep; propodus subrectangular, 2.9 times as long as deep, not broadly lobate; palm transverse, with convex margin; posterodistal corner with 1 medial spine.

*Peraeopods 3–7:* with short, slender dactyli. *Peraeopod 3:* simple; coxa extremely reduced. *Peraeopod 4:* simple; coxa extremely large, produced anteriorly and posteriorly, anterior margin convex, posterior lobe produced as far as coxa 6. *Peraeopod 5:* coxa shallow,

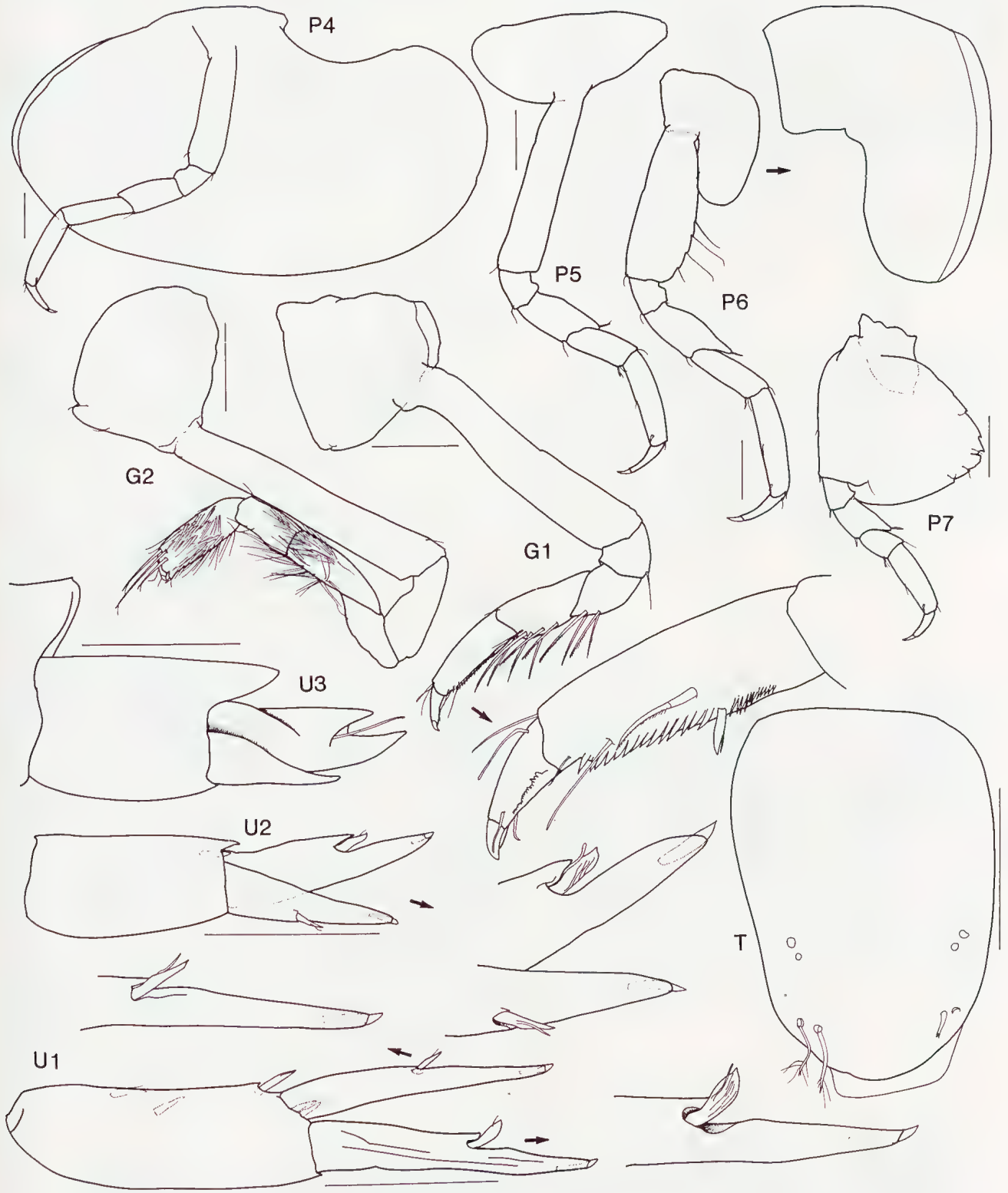


**Fig.7.** *Pseudocyphocaris lobata* n.sp., holotype, 2.2 mm, AM P39216, Gosem Island, Papua New Guinea. Scales represent 0.1 mm.

broader than deep, tapering posteriorly, not lobate; basis linear with posterior margin straight. *Peraeopod 6:* coxa small, greatly lobate posteriorly, basis linear, broader than basis of peraeopod 5. *Peraeopod 7:* basis extremely expanded posteriorly, subtriangular posterior margin crenulate, with a long slightly rounded posteroventral margin; merus slender, only slightly expanded posteriorly. *Oostegites:* from gnathopod 2 to peraeopod 5. *Gills:* from gnathopod 2 to peraeopod 7, not pleated.

*Epimeron 3:* with a small tooth on posteroventral corner. *Uropod 1:* outer ramus slightly longer than inner with large striated spine inserted in deep cleft; inner ramus with simple spine in shallow cleft. *Uropod 2:* peduncle elongate; outer ramus slightly longer than inner with large striated spine inserted in deep cleft; inner ramus with simple spine in shallow cleft. *Uropod 3:* peduncle short, 1.7 times as long as deep with lateral flange; rami lanceolate; inner ramus 0.7 times as long as outer ramus; outer ramus 1-articulate, broad with a subapical incision; plumose setae absent. *Telson:* 1.4 times as long as broad, entire, without dorsal spines, distal margin rounded, with 2 pairs of subapical penicillate setae.

**Remarks.** *Pseudocyphocaris lobata* and *P. gosema* both have posteriorly lobate coxa 6, but they differ in the development of the lobe and in the number of articles in the maxillipedal palp. *Pseudocyphocaris lobata* is related to *Wandin griffini* in two important ways. It has the same colour pattern and the vestigial dactylus on the

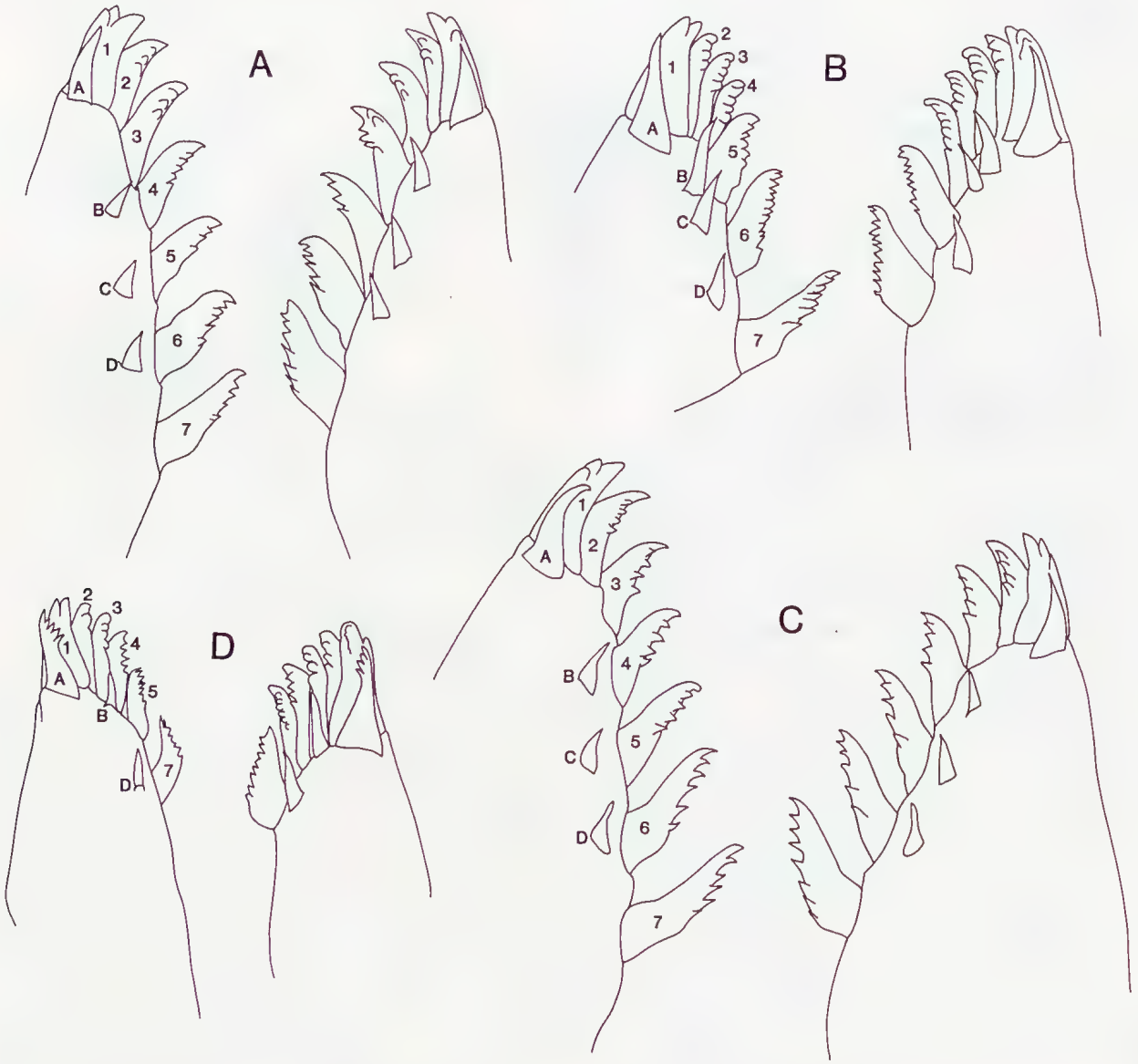


**Fig.8.** Examples of spine-tooth arrangements on the outer plate of maxilla 1. Outer row spine-teeth are labelled from the internal margin (ST1) to the medial margin (ST7). Inner row spine-teeth are labelled in a similar way, medial margin (STA) to lateral margin (STD). A: *Pseudocyphocaris coxalis* Ledoyer, MNHN Am 3988; B: *Pseudocyphocaris lobata* n.sp., AM P39216; C: *Pseudocyphocaris gosema* n.sp., AM P39215; D: *Wandin griffini* n.sp., AM P39209.

maxillipedal palp is present. These character states emphasise the phylogenetic similarity between the genera.

**Etymology.** The specific name refers to the unusually large posterior lobe on coxa 6.

## Wandinid Evolutionary Trends

The family Wandinidae is a monophyletic group of taxa which exhibits strong evolutionary trends towards commensalism. Members apparently have no secondary sexual characters. The peduncle of antenna 2 has a peculiar hook-like process. The mouthparts are long and slender, forming a conical bundle, and individual mouthparts are simplified in various ways. The anterior coxae are variously reduced in size and the bases of peraeopods 5 and 6 are slender. Coxa 4 is produced anteriorly and posteriorly to cover most of the side of the body.

There are striking similarities between wandinids and anamixids. Both groups live in tunicates. Thomas and Taylor (1981) reported *Anamixis hanseni* Stebbing from the tunicate *Ecteinascidia turbinata* Herdman. J.D. Thomas has seen *Pseudocyphocaris gosema* and *P. lobata* sitting on the lip of the tunicate *Didemnum molle* (personal communication).

Both groups have reduced anterior coxae. In *Anamixis hanseni* and *Wandin griffini* the first coxa is extremely reduced, and in *Pseudocyphocaris* coxae 1 to 3 are extremely reduced. From discussions with Thomas it appears that the size reduction of the anterior coxae allows the head to be tucked back under the body into a feeding position.

Both groups apparently have a mechanism for locking the head in place. According to Thomas (*in litt.*) in anamixids the lateral margins of the head and peraeonites 1 and 2 are produced in such a way as to lock the head between the coxae during feeding. The hook-like structure on the peduncle of antenna 2 in all wandinid taxa so far described may lock the head in a similar position.

Both groups have large coxae which form a lateral shield. In *Anamixis hanseni* coxae 2 to 4 are enlarged to form a lateral shield which probably helps direct pleopod-generated feeding currents (Thomas & Taylor, 1981). In *Wandin* the same coxae form the shield, but in *Pseudocyphocaris* the fourth coxa is extremely enlarged anteriorly and posteriorly to produce the shield. In wandinids the lateral shield projects posteriorly to peraeopod 7 and the bases of all peraeopods except 7 are slender. Coxa 4 may act in the same way as coxae 2 to 4 in anamixids and channel pleopod-generated feeding currents to the mouthparts.

One apparent contradiction in this hypothesis is that male anamixids have rudimentary mouthparts and wandinids have well developed mouthparts. However, female anamixids (leucomorphs) and leucothoids have well-developed subquadrate mouthparts and feed in the same way as male anamixids. It could be argued that wandinids feed by piercing and sucking or are mucus feeders, but the majority of existing morphological evidence indicates that they have a feeding strategy more similar to anamixids.

All of these adaptations apparently result in an efficient feeding mechanism for a tunicate commensal. Thus wandinids appear to be the lysianassoid equivalent of anamixid leucothooids. They show a number of examples of parallel evolution which have produced striking morphological similarities and apparently resulted in two unrelated groups filling similar habitats as tunicate commensals.

Acknowledgments. We thank Jim Thomas for giving us his lysianassoid collections to study and for allowing us to use his unpublished data on functional morphology in anamixid amphipods. We thank Steve Keable and Roger Springthorpe for valuable assistance with illustrations and plates. We thank Drs B. Meehan and P. Sutton for giving us the aboriginal name Wandin. Collections made by Jim Thomas were supported by grants from the National Geographic Society and the Smithsonian Institution. This study was supported in part by a grant from the Australian Research Council.

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# The Mammals of Southern West Sepik Province, Papua New Guinea: their Distribution, Abundance, Human Use and Zoogeography

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Abstract. A mammal survey was carried out between 1984 and 1987 in southern West Sepik Province, Papua New Guinea. Eleven major collecting localities, as well as some more minor ones, lying at altitudes of between 120 and 3,200 m were investigated. Voucher specimens for 87 indigenous mammal taxa were obtained, but research suggests that mammal diversity in the area may be as high as 120 species. This is the highest mammal diversity recorded anywhere in Australasia. A similar high bird diversity suggests that the area may be one of exceptionally high biodiversity overall. The most diverse mammal assemblages in the study area are found in the midmontane oak forests (between 1,500 and 2,500 m). Seven species, which apparently have no ecological vicars elsewhere in PNG, inhabit these forests. Changing patterns of human exploitation endanger some species. Recommendations aimed at halting this decline are made. The effect of the introduction of cats in one area was assessed as cats were introduced in the middle of the survey period.

Flannery, T.F., 1990. The mammals of southern West Sepik Province, Papua New Guinea: their distribution, zoogeography, human use and abundance. Records of the Australian Museum 42(2): 173–208.

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The aim of this work is to provide a comprehensive account of the mammals of the study area. First, there will be an account of the collecting localities and methods, then an annotated systematic list, and finally a synthetic discussion of several subjects of general interest, including an account of the zoogeography of the mammals of western New Guinea, the impact of introduced species, and the impact upon mammals of traditional and changing patterns of human use. It also offers solutions to conservation problems, and pinpoints areas of particular biotic significance. Data relating to reproduction and diet, and nesting sites etc. are not re-iterated here in detail, but can be found in Flannery *et al.* (1990).

The area chosen for this study lies between 4°30'S and 5°15'S, and 141°06'E and 141°45'E (Fig.1). Although a small study site (5,200 km$^2$), this region covers much of the homeland of Telefol, Mianmin, Atbalmin and the northern edge of the homeland of the Wopkaimin peoples. The area lies on the northern slopes of the New Guinean Central Cordillera (almost entirely within the northern watershed), almost in the geographical centre of the island of New Guinea. The topography is mainly mountainous, varying between 100 and 4,015 m in altitude (Fig.2). Although incidental collections of mammals have been made in this region in the past, this work represents the first attempt to fully survey its mammals. In all, some 87 mammal taxa were sampled by us, and it is estimated that up to 120 mammal species inhabit this region.

The mammal survey was carried out over four years, with repeated visits to the area being undertaken by the investigators (see Table 1). Only four areas were visited twice or more (Telefomin, Tifalmin, upper Sol River Valley, and the Yapsiei/Betavip area). However, these visits were extremely useful for investigating seasonality and other changes in the mammal fauna.

A wide variety of sampling techniques was used. Much material was collected by local people and purchased by expedition members. Elliott, Conybeare, conventional rat traps and mist nets were also set, and larger mammals were hunted using a spotlight and shotgun. Caves were also explored extensively for bats. Table 2 lists the mammal species obtained and gives our best estimate of some aspects of their biology.

There were several gaps in our altitudinal sampling due to lack of suitable access. Perhaps the most serious is that between approximately 400 and 900 m, where very few mammals were obtained. Because of this it has been difficult to determine the upper and lower altitudinal limits of some foothill-inhabiting species in our study area.

## Materials and Methods

The naming of vegetational types (where capitalised) conforms to Paijmans (1976). Colours in the new subspecies description follow the nomenclature of Smythe (1974). A list of Telefol and Mianmin mammal names is given in Table 3. Common English names for mammals follow Flannery (1990). All specimens collected during this survey are housed in the Australian Museum or the Papua New Guinea Museum and Art Gallery. The higher-level classification of the New Guinea bandicoots follows Flannery & Groves (in press). The Appendix contains all tables referred to throughout the text.

## The Study Area

**People.** Much of the study area falls within the 1980 census district 04 (Telefomin). The census divisions that lie within this district and their human populations are as

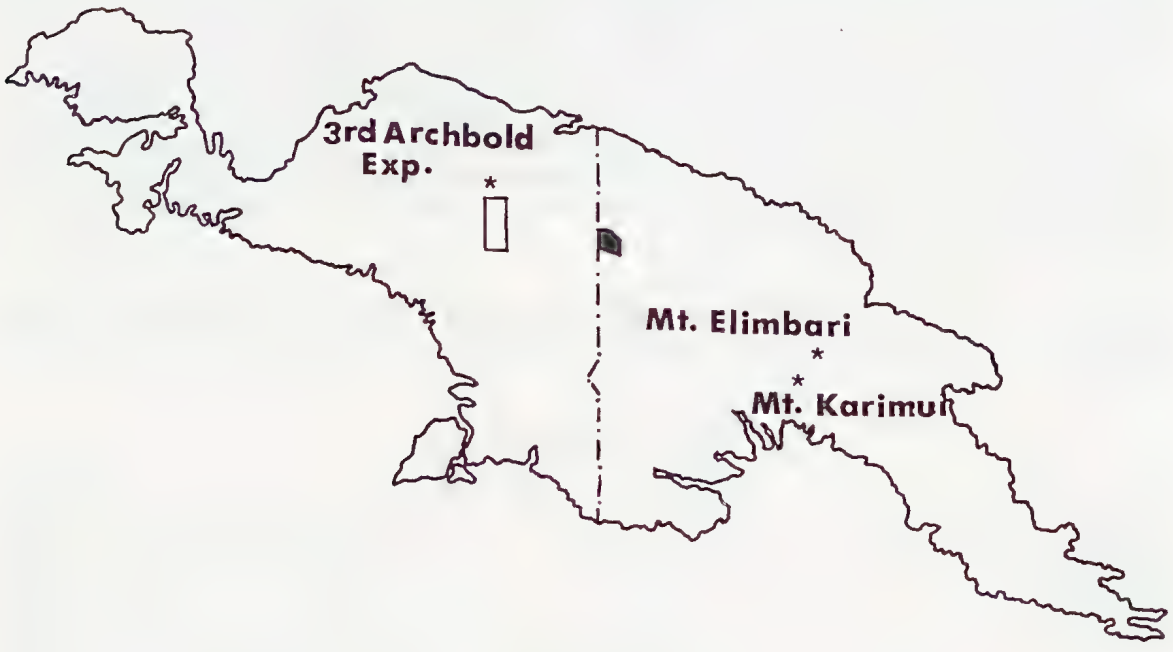


**Fig.1.** Map showing our study area (in black) and other locations mentioned in the text.

follows; Yapsiei local (491), West Mianmin (802), Atbalmin (2,245), East Mianmin (935), and Telefomin local (5,195), making in all about 10,000 inhabitants.

In the Yapsiei local, East and West Mianmin and Atbalmin census divisions the population is low and people tend to be spread rather evenly in small villages, although some larger population centres do exist. The Telefomin local district holds over half of the people in the area, who tend to be concentrated in the Telefomin, Elip and Ilam Valleys. Here, disturbance through gardening and hunting is at its maximum.

**Rainfall.** Some rainfall figures exist for Tifalmin, Yapsiei and Telefomin stations. However, data is limited and discontinuous, and all of the Tifalmin data, as well as substantial extracts from that for the other localities, is presented in Table 4. The figures for Yapsiei may be unreliable due to the absence of some daily recordings (R. Attenborough, personal communication). Despite these limitations, it seems that rainfall at Tifalmin is lower than elsewhere in the study area. This was our general impression in the field, and was supported by the observations of the local people. Yapsiei may receive a slightly higher rainfall than Telefomin. There is little suggestion of seasonality in rainfall, although there may be a mid-year peak at Yapsiei.

**Major collecting localities.** The major collecting localities are shown in Fig. 3. The village of Oboblikmin that is shown is the one located in the Ilam Valley. The Oboblikmin village near Mianmin (which is to the north of the study area) is not shown, being a minor collecting station.

**Yapsiei Station and the August/Sepik floodplain.** This area was the lowest altitude habitat sampled, parts of the August River floodplain lying as low as 120 m, with the highest parts of the sampled region lying at about 240 m.

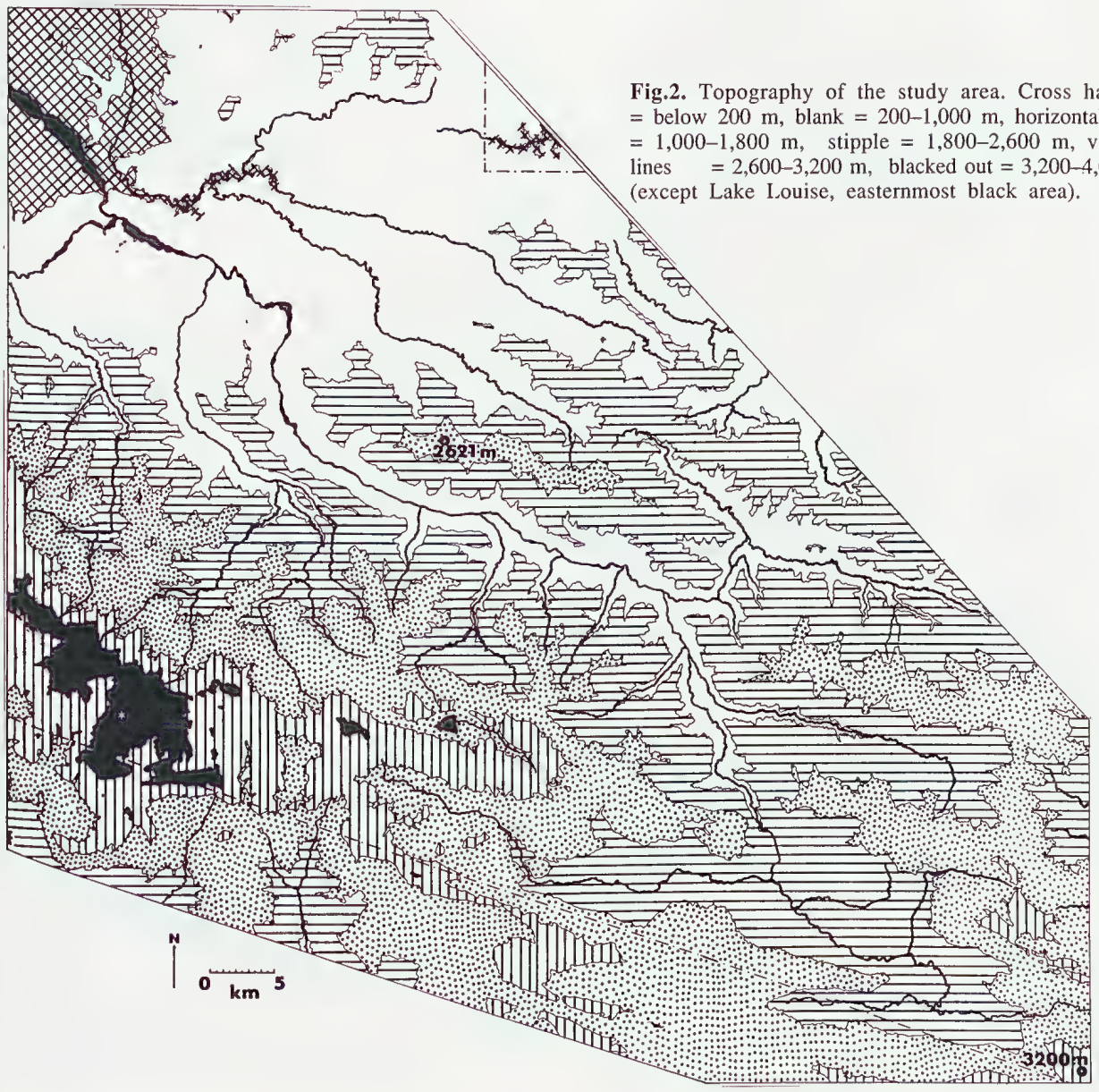


**Fig.2.** Topography of the study area. Cross hatched = below 200 m, blank = 200–1,000 m, horizontal lines = 1,000–1,800 m, stipple = 1,800–2,600 m, vertical lines = 2,600–3,200 m, blacked out = 3,200–4,000 m (except Lake Louise, easternmost black area).

Rainfall at Yapsiei Station is high (5,000–7,000 mm per annum) with only slight seasonality. Most collecting sites were on the flat-lying alluvial floodplain of the August River. Downstream from Yapsiei Station, this area is largely uninhabited and is only visited during occasional hunting forays. Here, a climax Mixed Alluvium Forest community is developed. Hunting and limited trapping with Elliott traps were the sampling methods used. The forest in the vicinity of Yapsiei Station is disturbed to varying degrees. The Station itself is located on the margin of the floodplain at 200 m, and is inhabited by approximately 450 people (1986) as well as a variable number of refugees. Disturbance ranges from total forest destruction and maintenance of a short, lawn-like grassland on the airstrip and around the main government buildings, to both current and regrowing gardens, through to forest which is being cut over for building materials and firewood. The government station was established at Yapsiei in 1973, and before this the area was not permanently inhabited and was little disturbed. Only limited and largely unsuccessful hunting was undertaken here, and some trapping using both Elliott and snap traps was carried out. However, an extensive mistnetting program was undertaken, primarily in gardens, disturbed forest and around government buildings.

**Betavip Village.** The village of Betavip is located approximately 14 km east-north-east of Yapsiei Station. However, the only access is along the meandering August River, and the walk is about one and a half days. It is a largely traditional Mianmin village of about 80 inhabitants (with a further 130 in the surrounding area). The village is positioned in a broad and isolated area of riverflats near the junction of the Skgonga and Usake Rivers. Where not disturbed, the alluvial flats support a climax Mixed Alluvial Forest. Disturbance is limited to current and regrowing garden areas, and some localised disturbance associated with the village and attempts to

Fig.3. The study area, with collecting localities marked (stars) as well as major topographic features. The dotted line marks the north-south divide.

define an airstrip near the village. Even close to the village there is ready access to climax forest on the floodplain margin and surrounding foothills.

This village was our major basecamp during January 1984 and April 1986. We carried out extensive hunting, trapping and mistnetting. We also employed Mianmin women to collect small mammals and men to hunt larger game, mostly in the 200 to 400 m altitudinal interval.

It seems likely that Betavip Village came into existence in the late 1960's when government patrols became frequent enough to suppress the feuding that necessitated the building of ridgetop villages. However, it is probable that some gardening was always carried out on the Betavip alluvial flats. Thus intensive exploitation of the Betavip area probably dates back less that 20 years.

A number of changes were noted in the Betavip area between 1984 and 1986. These include the translocation of the entire village approximately 1 km to the north-east, the clearing of a long, narrow band of climax or old Secondary Forest to define the space necessary for an airstrip, and the introduction of cats (see discussion). The total population had also grown due to the movement of Mianmin away from Yapsiei Station to locations further upstream on the August River.

**Mount Bubiari.** Mount Bubiari is the highest peak in the vicinity of Yapsiei and Betavip. Its summit (1,200 m) was investigated briefly during 1984, while hunting forays were made to the lower slopes during 1986. Hunting was the only collecting technique utilised successfully in the area. The 1984 basecamp was established at 900 m, hunting taking place over the altitudes 700 to 1,200 m, while in 1986 most hunting was done over the 400 to 600 m range. Most of the mountain is clothed in climax Mixed Evergreen Forest, although there are some areas of old secondary growth and abandoned village sites as high as 900 m and at least 20 years old. No *Araucaria* are present and the forest is dominated by large-fruited *Castanopsis*. The area is now visited only during occasional hunting forays by Mianmin. The terrain is steep and often rocky, and there is little undergrowth. The forest is stunted and mossy at the summit.

**Yominbip Village and the Thurnwald Range.** The village is a small, long-established settlement that is at present only intermittently occupied. It is perched atop a steep ridge at 1,000 m on the northern slopes of the Thurnwald Range. Small garden areas are located on the steep surrounding slopes, but there is little flat-lying gardening land available. Climax Mixed Evergreen Forest is abundant close by. The forest is unusually mossy for such low altitudes, particularly on the surrounding ridgetops at 1,300 m. *Araucaria* are absent, but a species of *Phyllocladus* is common in the area even as low as 900 m; *Castanopsis* species are abundant throughout. Low lying, persistent cloud and associated lowered temperatures were a common occurrence during our stay. Trapping and hunting were carried out extensively in climax forest, with some trapping and mistnetting taking place in disturbed patches.

The upper slopes of the Thurnwald Range (1,800–2,000 m) were visited by one of us (L.S.) for a week. This area is uninhabited, and had not been visited in recent years. Hunting and mistnetting were undertaken.

**Munbil Settlement.** Munbil is located at 900 m in the northern foothills of the Star Mountains. It is a new settlement, being carved out of climax Mixed Evergreen Forest during 1985. At the time of our visit in May 1986 the airstrip was still being lengthened and the newly-made gardens were beginning to produce crops. The settlement is situated on a large flat plateau between the Nong and Atem Rivers and is surrounded by extensive tracts of undisturbed climax forest. The area has a considerable population of Atbalmin which is still growing. The vegetation is far less mossy than at Yominbip and is more typical of lowland forest. No *Phyllocladus* are present, but *Araucaria* clothe nearby ridgetops above about 1,400 m. Limited hunting and extensive mistnetting and trapping were undertaken here. Unfortunately, many traps were set in gardens, and little trapping was successful in primary forest. Small murids were, however, collected by Atbalmin women. Mistnetting was carried out both in disturbed areas and climax forest.

**Telefomin Valley.** The Telefomin valley supports a human population of 800 to 1,000 people. A large part of the work in this area was carried out in the vicinity of Telefolip and nearby Bogalmin villages, in the most densely-populated central region, and at Ofektaman in the north of the valley. The valley floor consists of a plateau of flat-lying but deeply eroded Quaternary sediments. The plateau lies between 1,400 and 1,500 m, with the Sepik and its tributaries incising it to a depth of about 400 m. In the centre of the valley the plateau supports an anthropogenic grassland, while the small gullies support Secondary Mixed Evergreen Forest in various stages of disturbance. Disturbance usually consists of treefelling for firewood or building materials, but some gardens are also located here. *Araucaria* persist near the sacred village of Telefolip, where they are protected by tradition. Indeed, young plants are relocated and tended here by Telefol.

The history of vegetational change in the Telefomin valley over the past 60 years can be reconstructed with some accuracy. When the explorer Ivan Champion first saw the valley in 1926, it was a mosaic of grassy and forested areas, with the grassland mainly on the plateaus (personal communication). When the present airstrip and station was constructed in 1945 at least part of the ground had to be cleared of climax Mixed Evergreen Forest (if local informants are correct). Today clearing proceeds apace. A sawmill is located on the northern edge of the valley, where some of the last climax forest remaining on the plateau margin is being felled. The remaining forest relics in the central part of the valley are coming under increasing pressure for firewood, building materials and gardening. They are doubtless shrinking, with the smaller ones disappearing. Extensive hunting, trapping, mistnetting and foraging by Telefol were carried out

during 1984, 1985 and 1986. Many caves were also explored for bats.

**Tifalmin area.** Tifalmin lies in the valley of the Ilam River, with the flat river valley at about 1,300 to 1,400 m. This area was briefly visited in November 1984, and then more extensively investigated in April 1987 and March 1990. The 1980 census gives a population of 326 for the Tifalmin/Bafunmin area. Settlements are scattered throughout the valley, and much of the valley bottom and sides up to 1,700 m are anthropogenic grassland. Some gardens are located on the valley floor, but many are concentrated in a band of disturbed forest at about 1,800 m on the south side of the valley. A noticeable deterioration in the extent of forest cover was noted between 1984 and 1987. However, near the village of Oboblikmin at the eastern end of the valley extensive areas of lowland type rainforest still remain. These shelter *Phalanger orientalis* and other typical lowland species. This type of forest must have existed at some time further up the valley towards Tifalmin, but now only small remnants on very steep ground remain. Our impression, confirmed by local people, was that the Tifalmin area was considerably drier than the Telefomin Valley. Limited rainfall figures would tend to support this.

Extensive hunting was undertaken on the southern slopes of the valley near Tifalmin, at altitudes between 1,800 and 2,400 m, and at Oboblikmin and in low altitude forest remnants near Tifalmin. Trapping was also carried out in the valley floor and in forest at 1,800 m. The numerous caves in the valley were also explored.

**Nong River Valley/Miptigin ridge.** The Nong River is a small tributary of the Sepik which drains the Inim Range (not the Nong near Munbil). Its headwaters lie to the south-east of Telefomin, and the river flows eastwards to join the Sepik near Feramin. The valley floor near our 1985 basecamp is at 1,500 m. There is no permanent human habitation in the valley, and little disturbance to the climax Mixed Evergreen Forest that clothes it. This is because the area lies on the boundary of the Telefol homeland, and in traditional times was a dangerous place to visit as it was open to surprise attack. There are some *Araucaria*, but the forest is dominated by oaks (*Castanopsis* spp). Fogs were uncommon, and the sky was clear and weather warm during our stay (June). My impression is that the Valley of the Nong River is in a rainshadow, and experiences drier and warmer weather than the Telefomin Valley.

The valley sides are steep, but the floor has extensive flat areas. Extensive hunting, trapping and foraging by Telefol were all carried out in the valley, mostly at below 1,600 m. Limited mistnetting was unproductive, but a number of caves produced Microchiroptera.

Part of the northern rim of the Nong River Valley is a ridge called Miptigin. At our 1985 campsite it rises to 2,100 m, and this area was investigated for several days during 1985. It is dominated by a mossy climax Lower Montane Forest but with some disturbance and anthropogenic grassland along its northern margin. *Phyllocladus* is common, and other podocarps present; moss and epiphytes are abundant. Trapping and hunting were undertaken here.

**Sol River Valley.** The Sol River Valley is a westwards, then southwards-flowing tributary that enters the Sepik east-south-east of Telefomin Station. Our basecamp during 1984 and 1986 was beside the westwards-flowing headwaters of the Sol at an altitude of between 2,200 and 2,300 m. The floor of the valley at this altitude is gardened by the inhabitants of TelefolipVillage. The valley walls rise sharply to the south, north and east enclosing a relatively flat-lying basin, and gardening is restricted to its lower parts.

Away from the gardened zone, the valley is clothed in climax Lower Montane Forest. Even at altitudes of 2,600 m large fruited *Castanopsis* are common. However, no *Phyllocladus* were seen. The forest does not become very mossy until 2,600 to 2,800 m. The lower part of the valley floor is dominated by gardens and secondary growth in various stages. No major environmental changes were noted between 1984 and 1986. Hunting and trapping were undertaken between 2,200 and 2,800 m, with mistnetting being restricted to between 2,200 to 2,400 m.

**Dokfuma Basin, Mount Capella.** Dokfuma is a small subalpine herbfield perched on the southern slopes of Mount Capella at 3,200 m. Our campsite was on the edge of the valley, and this was the highest habitat investigated during our survey. The region is uninhabited and has no history of use of any sort according to Wopkaimin informants. However, it is crossed by the Busilmin-Tabubil track, which has been used with increasing frequency since the development of the Ok Tedi Mine. The Dokfuma valley itself is a small frost hollow about 1 $km^2$ with gentle slopes. The valley floor is covered in subalpine herbs and ferns, with small clumps of treeferns and stunted *Rhododendron* bushes. The valley margins support an open *Dacrycarpus* woodland, with *Phyllocladus*, *Papuacedrus* and *Schefflera* being common. In sheltered areas nearby a dense and extremely mossy Upper Montane Forest is developed. Hunting, trapping and mistnetting were undertaken in and around the basin.

## Taxa Obtained

### Monotremata

### Tachyglossidae

#### *Zaglossus bruijnii* (Long-beaked Echidna)

Only two specimens of *Zaglossus bruijnii*, both trophy skulls, were collected during this survey. The skull of an immature animal was obtained from a European aid worker at Telefomin Station, and presumably originated from the area of the Telefomin Valley although the date of its collection is unknown. The second skull, from an adult,

was collected at Oboblikmin Village, near Mianmin Station, and was reported by Mianmin to have come from one of the higher peaks around Oboblikmin.

Although Mianmin from the vicinity of Yapsiei Station (altitude 200 m) know of *Z. bruijnii*, they report that it is not found in their area, but comes from higher altitudes. Similarly, Mianmin from Yominbip Village (altitude 1,000 m) report that the species is not found in the area of the village, but is occasionally caught on the ridges surrounding the village at altitudes above 1,300 m. The species seems to be absent from the Telefomin valley at present, but within historic times was found there, as various European informants have reported seeing animals there before the mid-1970's. It is likely that the influence of the Baptist mission at Telefomin has been a major cause of its decline, as non-Christian Telefol have extremely strict taboos regarding the killing and eating of this species. Indeed, it was guaranteed virtual complete protection in the area controlled by the Telefol in pre-Christian times. At present, however, it is hunted and eaten by many Christians; and others, while they will not eat or kill it, will, if they come across an animal, sell or give it to a less traditionally-minded relative or friend.

The restriction of *Zaglossus bruijnii* to high altitudes (above 1,300 m) in West Sepik Province is surprising given its records from much lower altitudes both in the west of New Guinea (Thomas, 1907) and south of the Papua New Guinean Central Cordillera (at 600 m, Aplin, personal communication). This absence is unlikely to be due to hunting pressure, as some of the Mianmin district has an extremely low (and declining) human population. We regard it as more likely to be a natural absence due to some ecological factors which are as yet unknown.

## Marsupialia

### Dasyuridae

#### *Dasyurus albopunctatus* (New Guinea Quoll)

*Dasyurus albopunctatus* was obtained at only two localities within the study area, the head of the Sol River, and the head of the Skgonga River. The specimen from the Skgonga was brought in as a fresh skull and skin to Betavip in April 1986, and was reported to have come from a campsite at about 1,000 m. Two specimens were trapped at the head of the Sol River; a subadult female taken in an Elliott trap baited with peanut butter in January 1984, and a subadult male taken in a rat trap baited with a partial *Rattus steini* carcass in March 1986. The second of these captures was made after the traps had been raided, presumably by this animal, and captured rats removed. The animal was finally trapped within 20 m of our base camp, which was inhabited by about ten people and a dog. This species is not eaten by Telefol, who consider it unclean due to its meat-eating habits. Most Mianmin spoken to indicated that this species has a patchy distribution, with it being almost invariably met with at some locations but totally unknown from many others.

#### *Antechinus melanurus* (Black-tailed Antechinus)

This species seems to be present throughout the study area, with records from between 200 and 2,300 m. It is, however, generally uncommon. Where data for capture are available, the animals were taken while climbing in low trees, or in nests in trees or bushes. Most captures were from secondary forest, with none certainly known to have come from primary forest. Specimens from lower altitude are larger than those from higher.

#### *Antechinus naso* (Long-nosed Antechinus)

The single specimen taken was captured in an Elliott trap at about 1,400 m near Ofektaman. The trap was set in primary forest.

### Peroryctidae

#### *Microperoryctes longicauda* (Striped Bandicoot)

This species seems to be restricted to altitudes above about 1,400 m in the study area, with two captures coming from the Sol River basin (2,200–2,400 m), a third from Ofektaman, (1,400–1,800 m), and the last from Tifalmin (1,600 m). The Sol River animals were both located in nests among tree roots.

#### *Peroryctes raffrayana* (Raffray's Bandicoot)

Four of the six specimens obtained were taken at 1,000 m at Yominbip, a further specimen near Kobobip Village (Betavip area) at about 600 m, and another specimen at Ofektaman (altitude unknown, but between 1,200 and 1,800 m). This pattern of altitudinal distribution broadly fits that reported by Tate (1948b) from the Idenburg River area, with animals most common at about 850 to 1,200 m. The four animals from Yominbip were speared at night by Mianmin lying in wait beside fruiting *Ficus*. These *Ficus* produce fruit at the base of the trunk and roots, and (in May) were bearing heavy crops. Mianmin note that they have a long fruiting period and are a favourite food source of *P. raffrayana*.

#### *Echymipera clara* (Dimorphic Echymipera)

This species was only encountered in the lower and middle foothill forests (200–400 m) but it appeared to be moderately common there. A female with a furred pouch young was taken near Tibip Village (Betavip area) in January 1984. In general this species is rarer than *E. kalubu* in the study area, and does not inhabit disturbed forest. No

specimens were taken at Betavip during our 1986 visit.

### *Echymipera kalubu* (Spiny Echymipera)

This species was encountered at the lower to middle altitude collecting localities and was sometimes abundant. In the Telefomin valley (altitude 1,440 m) and at Yominbip (altitude 1,000 m) only a single individual was collected, both in very disturbed situations. However, at Betavip Village during January 1984, 12 individuals were collected over 16 days from forest, regrowth and gardens. On a return visit in April 1986 the species seemed to be much rarer, only two individuals being captured over ten days (both being taken at some distance from the village). Cats had recently (1985) been introduced into the village (with two animals, a male and a female, being present during our stay). The Mianmin villagers attributed the scarcity of bandicoots (and also large spiny rats) to predation by cats. We could see no other reason for the decline, and indeed while hunting at night on several occasions saw cats prowling in the forest where before we had taken bandicoots. Before the introduction of cats, this species was probably an important food source to the people of Betavip.

### *Echymipera rufescens* (Long-nosed Bandicoot)

This is the rarest peroryctid in the study area. It is represented in our collections by only five trophy dentaries and a single subadult male. This last specimen was captured by workers while they were cutting grass around Government buildings at Yapsiei Station in May 1986. The five trophy dentaries were all obtained in 1984 from villages bordering the August-Sepik floodplain. Although hundreds of bandicoot specimens and trophies were obtained in foothill forest away from the floodplain, not a single specimen of *E. rufescens* was included among them. These data suggest a preference by this species for floodplain habitats, and possibly only grassland or grossly disturbed areas on the floodplain. It is almost certainly not an inhabitant of foothill forest.

## Macropodidae

### *Dendrolagus dorianus* (Doria's Tree-kangaroo)

### *Dendrolagus dorianus stellarum* n.subsp.

Figs 4–6, Table 5

**Type material.** HOLOTYPE, AM M17789, puppet skin and skull with dentaries of an adult male. Collected T. Flannery and L. Seri; western end of Dokfuma basin, 3,000 m, Star Mountains, Western Province, Papua New Guinea, 5°01'S 141°07'E, 6 Apr. 1987.

PARATYPES, AM M17790, puppet skin and skull with dentaries of an adult female. Collected T. Flannery and L. Seri; north side of Dokfuma Basin, 3,160 m, Star Mountains, Western Province, Papua New Guinea, 5°01'S 141°08'E, 2 Apr. 1987. AM M19463, subadult male (young of AM M17790) entire in spirit, data as for M17790. AM M16699, puppet skin and skull with dentaries of a subadult male (judging from testes size not yet reproductive). Collected T. Flannery; upper Sol River Basin, 2,800 m, West Sepik Province, Papua New Guinea, 1 Apr. 1986.

**Etymology.** Of the stars (L.), a reference to the Star Mountains, which is the type locality and most of the known habitat of this taxon.

**Diagnosis.** *Dendrolagus dorianus stellarum* n.subsp. differs from the remaining subspecies of *D. dorianus* in the following ways: smaller, particularly in dental measurements (Table 5, Fig.7); tail yellow, with long terminal tuft, contrasts greatly with darker body (tail dark, without terminal tuft in *D. d. dorianus* and *D. d. notatus*); no dark patch over shoulders such as seen in *D. d. notatus*; anterodorsal part of body covered in silver 'frosted' hairs, contrasts with more brownish hindquarters, which lack such frosting (only *D. d. mayeri* has similar frosting, but entire dorsal surface frosted over blackish background, hindquarters do not lighten as in *D. d. stellarum* n.subsp.).

**Description.** Variation in the paratype series will be discussed below in relation to the description of the holotype.

**Skin.** Skin of holotype represents an adult male with fully-developed testes. Muzzle black, covered in short, black hairs. Forehead covered in short, silver-tipped hairs, differs sharply from fur of neck in texture and colouration. Posterior part of cheeks with cinnamon tinge. Ears black. Front part of dorsum, including neck, close to clove brown but lightly tipped with silver. Silver tipping on dorsal surface of fore and hindlimbs more pronounced, largely obscures brownish underfur. Silverish hairs extend to bases of claws. Fairly well defined but narrow and dark dorsal stripe on posterior half of back, extending from midway up back to base of tail. Posterior half of back much lighter than anterior half, being Van Dyck brown tipped with burnt umber. Ventral surface, including scrotum, uniformly dark, between Clove Brown and Seal Brown. Base of tail encircled with Orange Ochraceous hairs, with remainder of tail being predominantly Ochre Yellow, with a short, dark underfur. Long brush of bright Ochre Yellow hairs extends 110 mm beyond tail tip. 2 hair whorls present, 1 on each flank, approximately 120 mm anterior to tail base (defined as margin of Yellow Ochraceous hairs). Orange Ochraceous hairs extend to distal side of cloaca. Paratype subadult male (AM M16699) extremely similar in colouration to holotype. Testes markedly smaller, animal evidently not yet reproductive. Differs from holotype in being slightly lighter shade on anterior half of body, slightly less reddish across posterior part. Tail brush only 85 mm

long, orange ochraceous hairs encircle cloaca, forming patch 30 mm in diameter.

Female paratype (AM M17790) differs markedly in coat colour from both males. Cheeks markedly more yellowish, forehead less silvery, forehead fur merges with fur of anterior part of back, rather than being sharply differentiated from it. Anterior part of back more densely tipped with silvery hairs, posterior part of back markedly more rufous, with rufous area extending further anteriorly. Tail with greater admixture of yellow hairs, tail tuft (95 mm long) Tawny Ochraceous at tip. Large cream buff spot on venter (130 mm in width, 65 mm in length), between pouch and cloaca, which is separated from tail base by band of dark hairs.

**Skull and dentition.** As a detailed description of the skull and dentition of a species of *Dendrolagus* has not been given previously, it has been included here. The skull of the holotype is little damaged, only lacking the left paroccipital process. The enamel of M2 is breached by wear.

*Dentition.* I1/ overhangs I2-3/, has largest diameter of upper incisors. I3/ is larger than I2/, occlusal surface V-shaped with apex oriented anteriorly. 2 small enamel cristae run posterolaterally from internal wing of 'V' to link with lateral one. Canines slightly laterally flattened with small

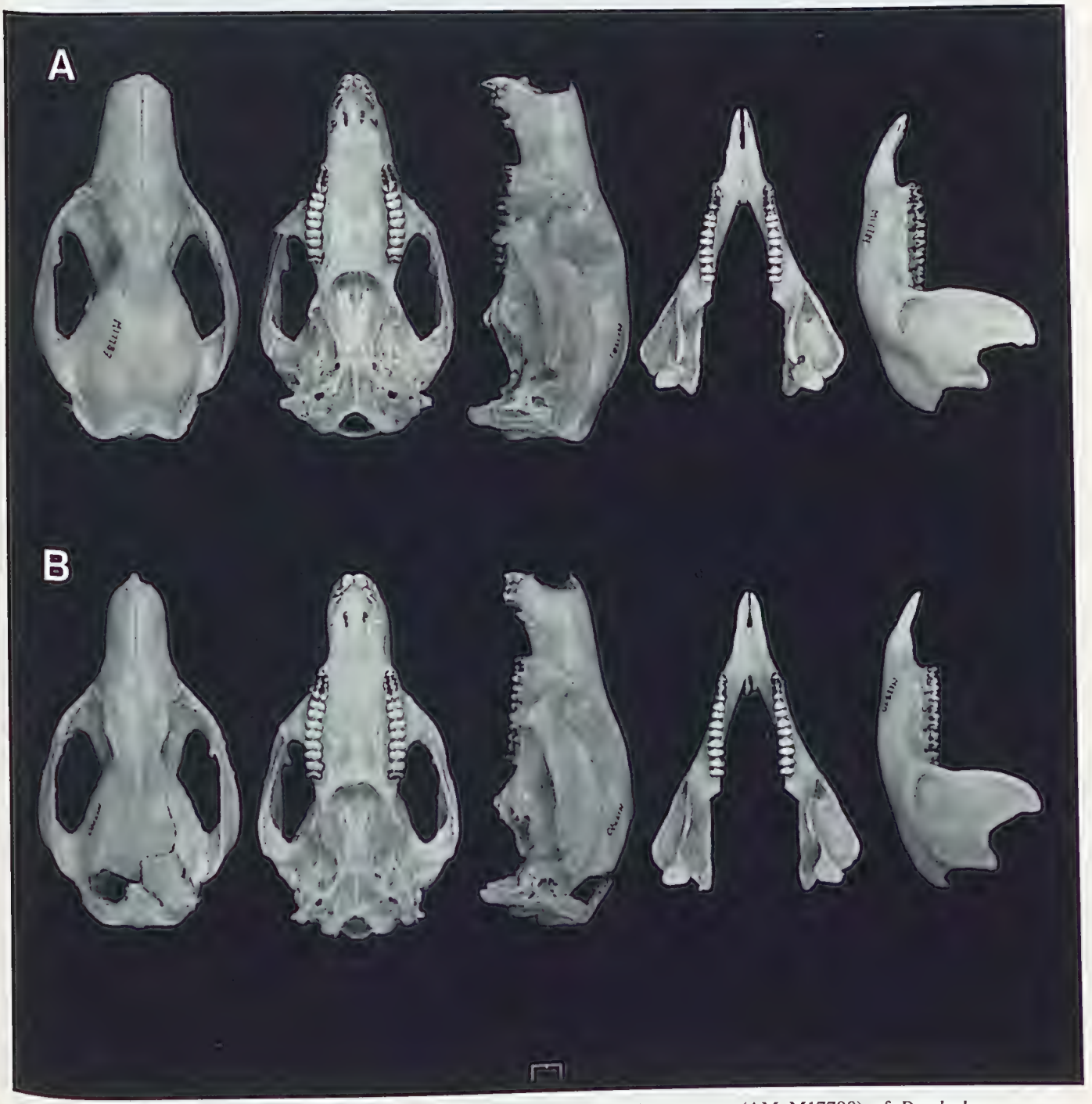


**Fig.4.** Skulls of A, the holotype (AM M17789) and B, female paratype (AM M17790) of *Dendrolagus dorianus stellarum* n.subsp.

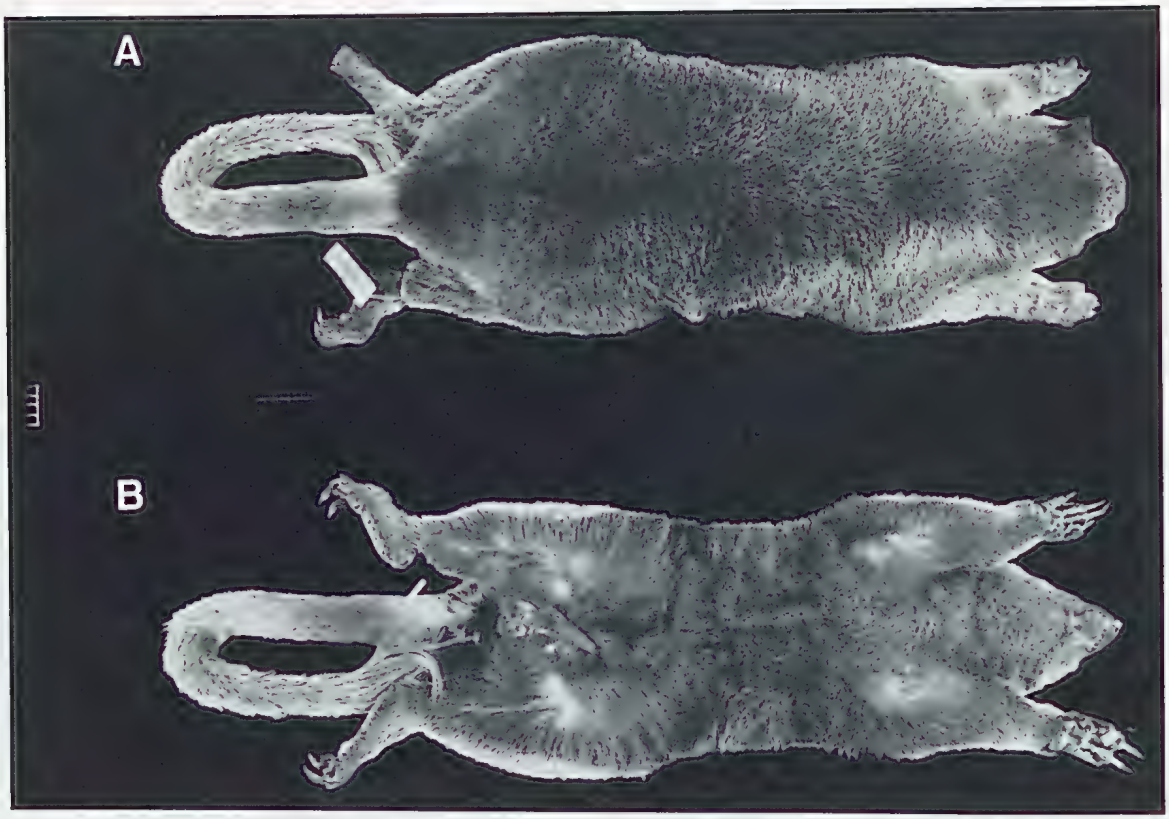


**Fig.5.** Study skin of the holotype (AM M17789) of *Dendrolagus dorianus stellarum* n.subsp. in A dorsal and B ventral views.

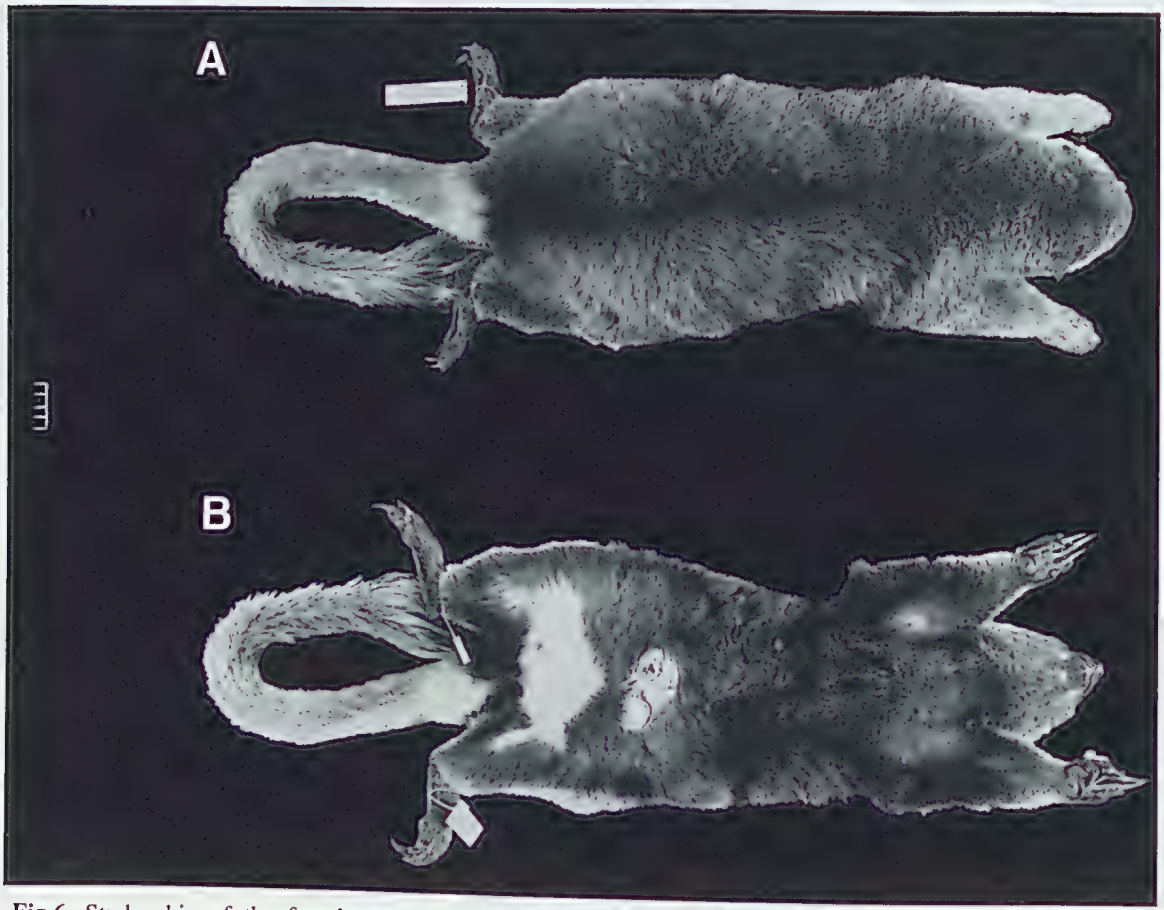


**Fig.6.** Study skin of the female paratype (AM M17790) of *Dendrolagus dorianus stellarum* n.subsp. in A dorsal and B ventral view.

'heel' at posterior of crown base.

P3/ composed of main blade ornamented by 4 cuspules, a lingual cingulum, a posterolabial and buccal cusp. Anterior and posteriormost cuspules of main crest larger than middle ones. Lingual cingulum moderately well developed. Posterobuccal cusp of left P3/ slightly less well developed than that of right, while posterolingual cuspules on both sides large.

M2/ a simple bilophodont tooth. Anterior cingulum narrow but distinct. All anteroposterior linking weakly developed. M3-4/ similar to M2/, except larger and anterior cingulae broader. M5/ differs from more anterior molars in having hypoloph markedly narrowed.

Lower incisors as in other *Dendrolagus* species. P/3 consists of main blade ornamented with 4 cuspules. Anteriormost the most prominent, divided from rest of tooth by a deep cleft. 2 central cuspules subequal in height, smaller than others, posterior cuspule large, bulbous, long axis deflected slightly posteromedially relative to other cusps.

M/2 a simple, bilophodont tooth with moderately developed paracristid and poorly-developed cristid obliqua. Anterior cingulum low although well developed. M/3-4 differ from M/2 in being larger with narrower anterior cingulae. M/5 closely similar to M/4 except hypolophid narrower.

*Skull.* Holotype skull represents a fully mature male, however sagittal crest only poorly developed. Frontals also only weakly inflated; much less inflated than any adult *D. d. mayeri*, *D. dorianus dorianus* or *D. d. notatus*. Nasals blunt ended (may have suffered some slight damage). Parietal region lacks heavy pitting present in *D. d. mayeri* and many adult male skulls of other subspecies.

Skull of subadult male paratype differs from holotype in being even smaller, although adult dentition fully in place. Sagittal crest not properly formed (parietal ridges

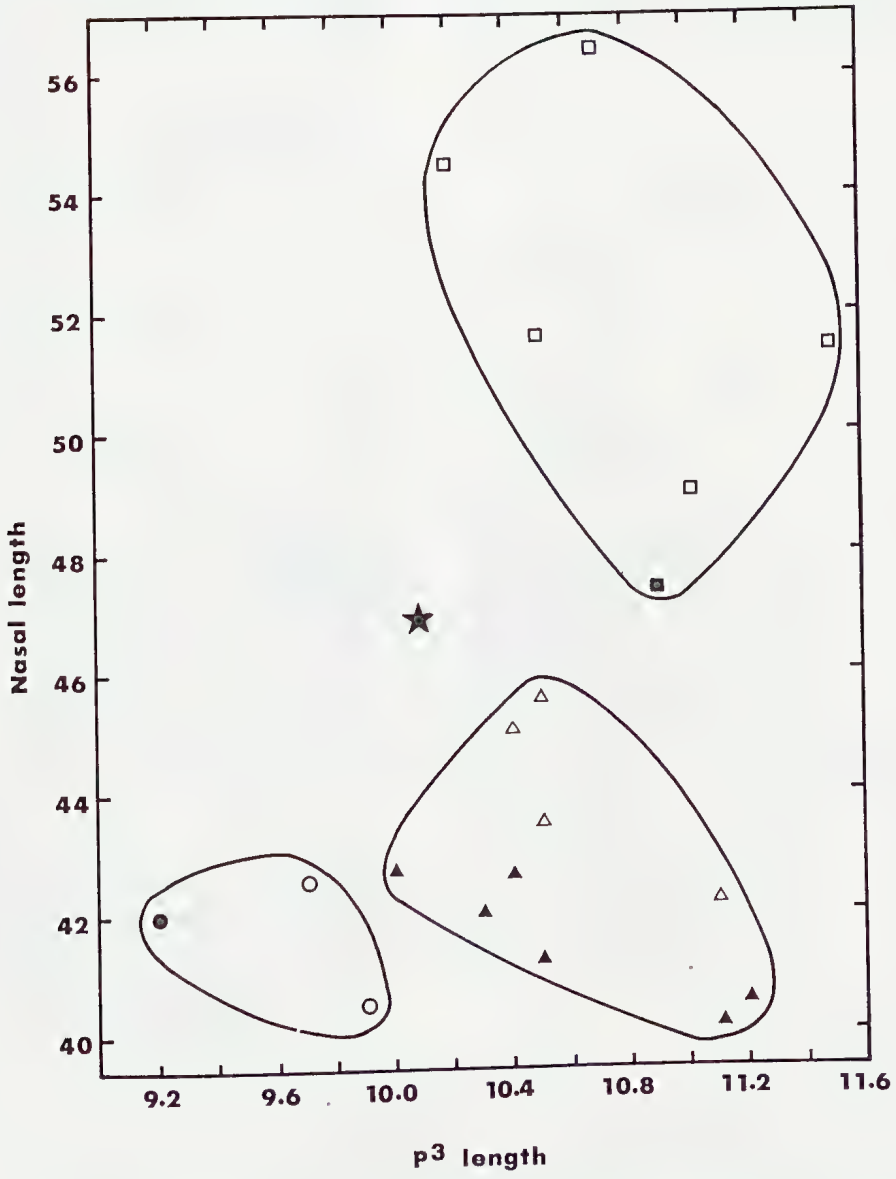


**Fig.7.** Bivariate plot of nasal length over P3/ length for *Dendrolagus dorianus dorianus* (squares), *D. d. notatus* (triangles), *D. d. mayeri* (star) and *D. d. stellarum* n.subsp. (circles). Solid shapes are for males and open shapes for females. All except *D. d. mayeri* (measurements supplied by Groves), are specimens in the AM collections.

not yet having coalesced), frontals completely unexpanded, indeed being somewhat concave.

Paratype female skull from reproductive animal. Similar in size to paratype male: remarkably narrow rostrum; parietal crest totally undeveloped, with parietal ridges being well separated; frontals concave as in paratype male. Overall, paratype female skull much more gracile than other adult *D. dorianus* skulls examined.

**Discussion.** Groves (1982) is a comprehensive and largely excellent revision of the genus *Dendrolagus*, based upon the majority of specimens in world museums. It is in the context of this work that the new subspecies is described here. The material examined by us in completing this work is as follows: all *Dendrolagus* specimens held in the Australian and Macleay Museums, Sydney, and the National Wildlife Collections, Canberra, which include the holotypes or lectotypes of *D. dorianus*, *D. spadix* and *D. deltae*; good quality colour photographs of the skin of the holotype of *D. d. mayeri* (kindly supplied by C.P. Groves); notes and measurements of specimens held in Leyden (also supplied by C.P. Groves), and the good quality photographs of the skulls of the holotypes of *D. d. mayeri* and *D. d. notatus* published in Rothschild & Dollman (1936).

*Dendrolagus dorianus stellarum* n.subsp. shares similarities with both of its nearest geographical neighbours — the subspecies *D. d. mayeri* from far western New Guinea, and *D. d. notatus* from the central highlands. It differs greatly from *D. d. dorianus* from far eastern New Guinea (see Diagnosis; Fig.7) and this subspecies will not be considered further here. *Dendrolagus dorianus notatus* is the subspecies that occurs closest to *D. d. stellarum* n.subsp. It is widespread throughout the central highlands of Papua New Guinea, occurring from Morobe Province in the east (Groves, 1982) to Mount Sisa, Southern Highlands Province in the west (e.g. AM M15723). Mount Sisa lies approximately 150 km east of Telefomin, which is the easternmost known occurrence of *D. d. stellarum* n.subsp. The consistent shape and size difference between the skulls of these subspecies (see Fig.7; Description above), and the distinctive morphology of *D. d. stellarum* n.subsp. (see Diagnosis and Description) suggest that they do not intergrade, but that perhaps their ranges are separated or abut. *Dendrolagus dorianus stellarum* n.subsp. is only known from altitudes in excess of 2,800 m, while *D. d. notatus* can be found below 1,000 m in the Mount Sisa area where altitudinal zones are depressed. It may well be that the Hak/Om low point on the Central Cordillera at 4°55'S 131°45'E (see Zoogeography **in** Discussion) acts as a barrier separating these subspecies.

*Dendrolagus dorianus mayeri* is known from a single specimen collected on the Wondiwoi Peninsula, which juts into Geelvinck Bay, 450 km to the west of the Star Mountains. This subspecies is morphologically the closest of named subspecies to *D. d. stellarum* n.subsp., both sharing small size and possessing bright yellow or ochre tails. However, they differ in cranial morphology, size and pelage colouration. The similarities between *D. d. stellarum* n.subsp. and *D. d. mayeri* are surprising as the Wondiwoi Peninsula is not part of the Central Cordillera, and is separated from it by several very low lying regions, including the Lake Jamur area and the Wissel Lakes. These landforms must be effective barriers for montane species such as *D. dorianus*. There are no records of living tree kangaroos from the Central Cordillera to the west of the Star Mountains despite intensive mammal collecting (e.g. see Archbold, Rand & Brass, 1942). The westernmost record for a living animal is that from Ok Bon, Mount Antares, in the Star Mountains (Groves, 1982) which is represented only by a skin held in the Leyden Museum. A description supplied by Groves suggests that it is almost certainly *D. d. stellarum* n.subsp.

Hope (1976) records a subfossil fragment referred to *D. dorianus* from Mapala rockshelter, Mount Carstenz (at 3,996 m) which is probably about 5,000 years old. The maxillary fragment (AM F54777) represents a small animal, closest in size among material examined by us to *D. d. stellarum* n.subsp., and it probably represents that subspecies. If *D. d. stellarum* n.subsp. has, as this very limited data may suggest, become extinct throughout most of Irian Jaya during the Holocene, then fears must be held for its continued existence in the Star Mountains area. Its range as currently understood covers only 90 km along the Central Cordillera from Mount Antares in the West to the Telefomin area in the East. Figure 8 shows our estimate of its distribution in Papua New Guinea. This figure is based upon extensive questioning of local peoples throughout the region and our own hunting results, and we are confident of its accuracy. In the Telefomin area, the species is absent from much apparently suitable habitat, which is almost certainly due to overhunting. Indeed, it seems to have been hunted out from all regions less than a full days walk from major settlements in our study area. Even in more remote regions it is rare. For example, two weeks of fieldwork in the upper Sol River Valley (which has a reputation among Telefol as a good place for finding the species) employing renowned tree kangaroo hunters, resulted in the capture of only a single specimen. However, it is currently common in the Dokfuma area of the Star Mountains, the most remote and rarely visited of sampling sites in our region.

A final point regarding its distribution needs to be made, for this species is absent from the Drei Zinnen Range of the study area. Although seemingly suitable habitat, its absence from this range may be due to lack of high-altitude access from the Central Cordillera (Fig.2).

Telefol respect many restrictions regarding the consumption of *Dendrolagus dorianus*. In general, only the most senior males are allowed to consume it. This was brought to our attention when AM M17790 was caught. Although several adult men were present at our camp in the Sol River when the animal was brought in, only one old Councillor was considered senior enough to eat it, the remainder of the meat being carried down the mountain to be consumed by three or four senior men at Telefolip.

### *Dendrolagus goodfellowi buergersi* (Goodfellow's Tree-kangaroo)

The distribution of *D. goodfellowi* was also mapped with some precision (Fig.8). As can be seen, it and *D. dorianus* are allopatric in the study area. This was a surprising find as further east these species are sympatric. The material reported upon here represents the westernmost occurrence of this species in New Guinea. It is restricted to altitudes above 1,000 m, and thus the Sepik forms a barrier to westwards expansion. Extensive questioning of Atbalmin informants (who had gathered at Munbil settlement for a health clinic) confirmed its absence from middle montane forest to the south of the Sepik. Curiously, however, several pieces of *bilas* (decorative material) incorporating tails examined by me indicate that it is present in the southwards-flowing Om River valley north of Telefomin. *Dendrolagus goodfellowi* from the study area are among the largest individuals of this species examined, being similar in size to *D. d. stellarum*. Further to the east, where *D. goodfellowi* and *D. dorianus* are sympatric, there is a marked size difference between the species.

As with *D. dorianus*, this species is sensitive to hunting pressure. We found it to be common at only one locality, Yominbip (1,000 m) in the Thurnwald Range. Here human population is low and declining and the species seems readily caught, even in the vicinity of Yominbip Village itself. Mianmin report that it is found high in the Thurnwald and Drei Zinnin Ranges, probably to the summit (about 2,600 m). Mianmin do not seem to respect any food taboos relating to this species.

### *Dorcopsis hageni* (White-striped Dorcopsis)

As with *Echymipera rufescens* this species seems to be restricted to the August-Sepik floodplain in the study area. Here, however, it is abundant, numerous trophy skulls and

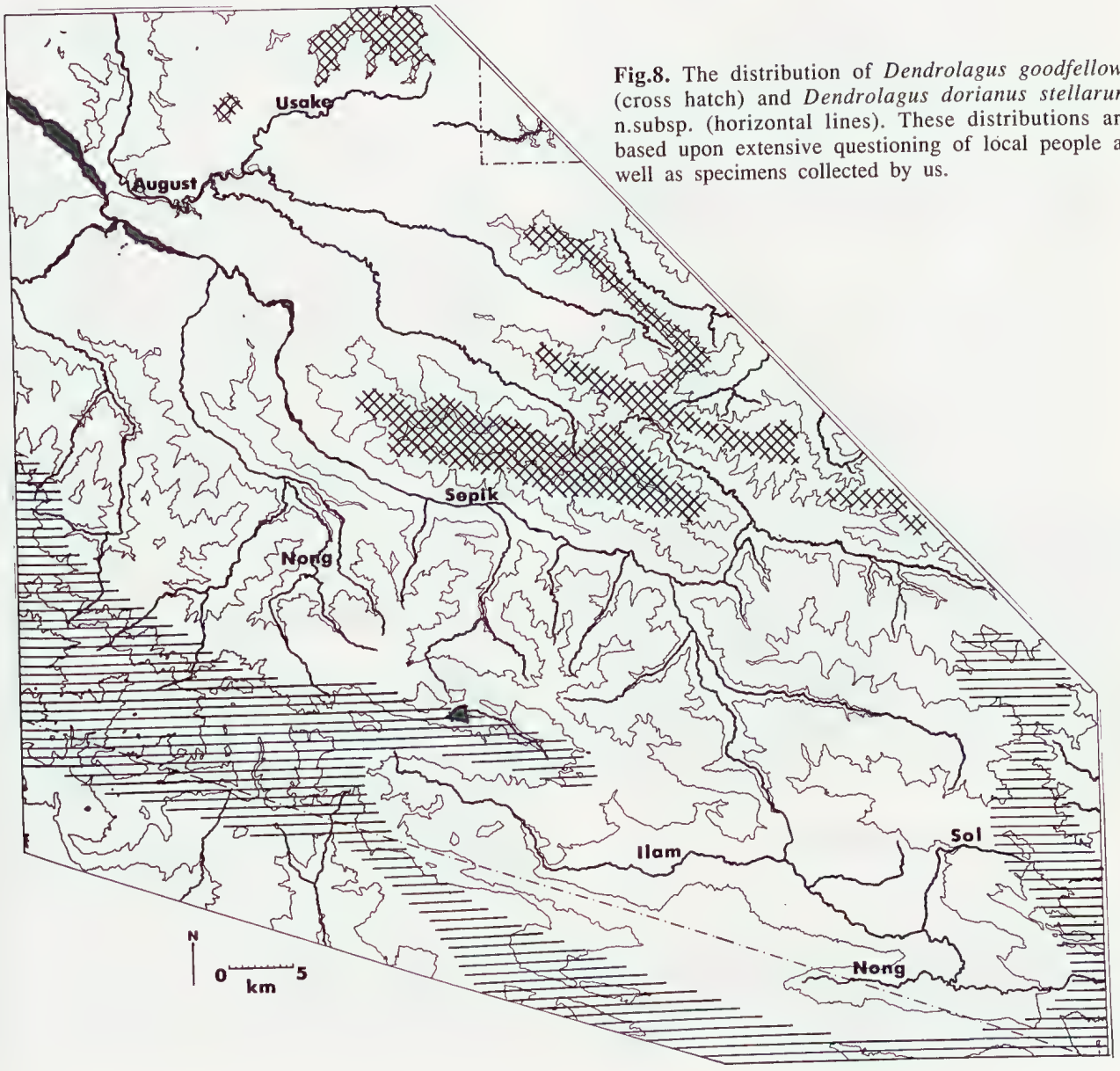


**Fig.8.** The distribution of *Dendrolagus goodfellowi* (cross hatch) and *Dendrolagus dorianus stellarum* n.subsp. (horizontal lines). These distributions are based upon extensive questioning of local people as well as specimens collected by us.

five whole animals being obtained during brief visits to the floodplain and its neighbouring villages. Extensive work in the low foothill and higher forest has failed to reveal its presence there. A number of Mianmin hunters suggested that two species of *Dorcopsis*-like animals were found on the floodplain. However, we found evidence of only one, which they indicated was the larger of the two 'folk taxa'. *Dorcopsis hageni* may represent an important source of protein for Mianmin who live in villages bordering the floodplain. It is abundant, and is often caught on shingle-banks along the August River, where the Mianmin say it comes to find insects under the shingles.

### *Dorcopsulus vanheurni* (Small Dorcopsis)

All six *Dorcopsulus vanheurni* collected during this study were taken at altitudes of 1,000 m and above, and according to Mianmin informants, 1,000 m is the approximate lower limit of its distribution in the study area. It appears to be common in montane forests between 1,300 and 2,300 m, and may extend to higher elevations, as the foot bones of a small macropodid (probably this species) were found in wild dog droppings at Dokfuma (3,200 m). Wallaby drives are held by Telefol, and informants have related to us that during a drought in the early 1980's a large section of the primary Oak Forest on the south side of the Nong River valley was set alight and approximately 400 *D. vanheurni* were caught as they fled before the flames.

### *Thylogale brunii* (Dusky Pademelon)

This species is rare in the study area and we obtained only a single freshly-caught specimen in foothill forest near Kyemana Village (about 600 m). Trophies were also collected, mostly from villages with access to forest in the 500 to 1,000 m range. This species is unknown in the Telefomin Valley, and is absent also from the higher peaks of the Central Cordillera as well as the Sepik floodplain. No droppings or other sign of this species were found in the Dokfuma herbfield, although in my experience such signs are abundant where the species exists in subalpine grassland in eastern New Guinea. Within the study area, it is often found in primary forest, but Mianmin have mentioned to me that it is most commonly encountered in areas of old landslips where vegetation is regrowing.

## Phalangeridae

### *Spilocuscus maculatus* (Spotted Cuscus)

The Spotted Cuscus is not common in this region. Our work resulted in the capture of only a single animal, from Kyemana Village (altitude 600 m) in the Betavip area. However, a number of trophy skulls were collected in the Yapsiei, Betavip and Yominbip areas. The Yominbip area (altitude 1,000 m) may represent the upper altitudinal limit of this species in the study area. The rarity of this species in the study area was unexpected and we cannot account for it. Elsewhere it is much more common and widespread than *S. rufoniger*.

### *Spilocuscus rufoniger* (Black-spotted Cuscus)

Specimens of this rare species were collected at 120 m on the August River Floodplain north of Yapsiei, at Kyemana Village (600 m), and on Mount Bubiari (1,200 m, probably its upper altitudinal limit in the study area). It was always encountered in primary forest. This species is sensitive to overexploitation by the use of shotguns (Flannery, 1990). However, as long as access to cartridges is limited in the Yapsiei area, and cultivation does not become too extensive, this species should continue to survive there.

### *Strigocuscus gymnotis* (Ground Cuscus)

The Ground Cuscus was the most commonly encountered phalangerid in the study area. It was also the most commonly represented animal in trophy collections. We did not encounter it on the August-Sepik floodplain, but found it as low as 300 m in foothill forest in the Betavip area. It was most common at altitudes of around 800 to 1,300 m, but remained as a less common element of the fauna to altitudes as high as 2,600 m. Specimens from above 1,800 m are conspicuously smaller than those from lower altitudes. They usually have denser fur and a light tail tip, features lacking in lower altitude specimens. Considering its abundance, broad distribution, large size, and susceptibility to indigenous hunting techniques it is likely that for the Mianmin at least, this species forms the most important mammalian portion of their diet. It is commonly hunted by day using dogs, but is also smoked out of burrows and shot at night.

### *Phalanger orientalis* (Common Cuscus)

*Phalanger orientalis* is the most commonly-encountered phalangerid in disturbed forest in the vicinity of villages in the study area. It is also, however, found in primary forest. Records are from as low as 120 m on the August floodplain, andas high as 1,500 to 1,600 m in the Thurnwald Range, although it probably extends higher there. It was also encountered in the floor of the Telefomin Valley at about 1,500 m, but not in the Nong River Valley at the same altitude. While the Nong River Valley is largely undisturbed Oak Forest the Telefomin Valley is a mosaic of grassland and disturbed forest. This may account for the differing altitudinal limits of this species in the two areas. In the Thurnwald Range, *P. sericeus* and probably *P. carmelitae* are absent, possibly allowing *P. orientalis* to reach higher altitudes there than elsewhere.

Because of its occurrence in disturbed habitats, particularly around villages and in old gardens, this species may be an important prey item for those who do not travel far to hunt (i.e. women).

### *Phalanger matanim* (Telefomin Cuscus)

Only four specimens of this newly-described *Phalanger* (Flannery, 1987) were collected during our study. One was from Oak Forest in the Nong River Valley (1,500 m), two from Tifalmin (1,600–1,800 m), and a further specimen from the upper Sol River Valley (2,600 m). This is a rare species, but is favoured by Telefol as a food item because of its subcutaneous fat.

### *Phalanger vestitus* (Stein's Cuscus)

This species was found at only four localities during the present study. A single trophy skull was collected at Yominbip in the Thurnwald Range, two animals were obtained at Ofektaman in the Telefomin Valley (1,400–1,600 m), two at Tifalmin (about 1,600 m), and eight were collected in the Nong River Valley (1,500 m). At the last-mentioned locality, *P. vestitus* was the most commonly-caught large mammal.

It seems that this species is susceptible to habitat disturbance. Older Telefol men have informed me that it was common in the Telefomin Valley itself in their youth, but has declined as clearing and gardening increased with the coming of European technology. Today, the species is rare if it occurs in the main part of the valley at all. It is restricted altitudinally, probably being found only in primary forest at between 1,400 and 1,600 m in the study area.

### *Phalanger carmelitae* (Mountain Cuscus)

This species appears to be uncommon in the study area, with only seven specimens being collected. One each were obtained in the Nong River Valley at 1,500 m, and Ofektaman (1,400–1,800 m), and three at Tifalmin (1,600–2,000 m) and two at Finimterr (2,200–2,400 m). Extensive collecting at 2,200 m and above in the Sol River Valley failed to reveal its presence there, which is curious, for in our small samples from Finimterr and Tifalmin (both relatively high altitude areas) it outnumbered the other *Phalanger* species. Tifalmin and possibly Finimterr are drier than other parts of the study area, and resultant vegetational differences may favour this species over *P. sericeus*. As with *P. matanim*, this species is prized for its subcutaneous fat deposits by Telefol.

### *Phalanger sericeus* (Silky Cuscus)

The Silky Cuscus is abundant at altitudes in excess of 2,200 m along the Central Cordillera in the study area. It is also found as low as 1,500 m in the Nong River Valley, where there is much primary forest. Here, however, it is rare. It is certainly absent at similar altitudes in the more disturbed Telefomin Valley. Above 2,200 m in the Sol River Valley it is by far the most commonly caught phalangerid.

It is concluded that this species is absent from the Thurnwald and Drei Zinnen Ranges for the following reasons. Through an east Mianmin interpreter (who was familiar with the species) we were able to question a large number of west Mianmin inhabitants of both the Thurnwald and Drei Zinnen Ranges regarding this species. All indicated that it did not exist in their area, although a few were familiar with it from visits to the Atbalmin or east Mianmin areas. In addition, no trophy material of this species came to light in the collections we made in this region. The absence of this species from the Drei Zinnen and Thurnwald Ranges is curious, and probably the same factors that account for the absence of *D. dorianus* from the area apply to this species also.

## Pseudocheiridae

### *Pseudocheirus mayeri* (Pigmy Ringtail)

This species was found only on the higher parts of the Central Cordillera within the study area. A specimen from Ofektamen may have come from as low as 1,800 m, but elsewhere the species was found at higher altitudes (Miptigin 2,000 m, Sol River Valley 2,200–2,800 m). A dentary fragment was also found in a wild dog dropping at Dokfuma (3,200 m). Between 2,200 and 3,000 m it can be locally abundant. This species is too small to be an object for trophy collection.

### *Pseudocheirus forbesi* (Painted Ringtail)

The Painted Ringtail is an extremely common animal in the area of the Telefomin and Tifalmin Valleys. Here, and possibly in the Thurnwald Range (based on questioning of local people), it probably occurs as low as 1,300 m. It extends as high as 2,300 m in the Sol River Valley, but at these altitudes it is rare. This species seems to be able to exist in small patches of secondary regrowth, and during our work it was regularly caught in such areas in the Telefomin Valley. It is also common in primary forest within its altitudinal range.

### *Pseudocheirops corinnae* (Plush-coated Ringtail)

This species seems to be present only within a very restricted altitudinal range, at about 1,800 to 2,200 m, and even here it is not common. A few specimens were brought in at the Sol River locality, but they seemed to come from the lower part of the valley (2,200–2,300 m). It is certainly absent from altitudes below 1,600 m, as

extensive work in the Telefomin and Nong River Valleys failed to reveal its presence there.

### *Pseudocheirops cupreus* (Coppery Ringtail)

This species has a curious distribution in the study area. Along the Central Cordillera we encountered it only at altitudes in excess of 2,300 m in the Sol River Valley and above 2,200 m at Tifalmin. At these altitudes, however, it was the most abundantly caught large game mammal. Limited work at slightly lower altitudes (Miptigin 2,000 m, Ofektaman 1,400–1,800 m) failed to reveal its presence there, so it is probably limited to the higher altitude areas of the Central Cordillera. However, this species is present in the isolated Thurnwald Range (Fig.2), where two specimens were captured at 1,800 to 2,000 m. As this species seems to have an even more restricted altitudinal distribution along the Central Cordillera than *P. sericeus*, its presence in the Thurnwald Range comes as a surprise. We have no explanation for this distribution at present.

Because it is so common and easily obtained, this species is probably an important element in the Telefol and Tifal diets. Its large numbers in the only trophy collection examined at Telefomin supports this hypothesis.

## Acrobatidae

### *Distoechurus pennatus* (Feathertail Possum)

Only three specimens of this species were obtained during our study. One was taken in a small tree in Ebolio Village (160 m), a second in a garden along the Sepik (120 m), and a third in the environs of Yominbip Village (1,000 m). It is probably absent at altitudes in excess of 1,000 m as extensive work in the Telefomin Valley has failed to reveal its presence there. This species was not encountered in primary forest, and seems to be primarily an inhabitant of gardens and disturbed areas. Hyde *et al.* (1984) also record it most often from such habitats on Mount Karimui.

## Burramyidae

### *Cercartetus caudatus* (Long-tailed Pigmy Possum)

The Long-tailed Pigmy Possum is most common at altitudes of above 2,000 m in the study area (i.e. Miptigin, upper Sol River Valley), but was also found at Ofektaman (1,400–1,800 m) and the Nong River Valley (1,500 m). A single specimen was taken in the Dokfuma herbfield (3,200 m) in a snap trap. It was encountered both in disturbed habitats and primary forest.

## Petauridae

### *Petaurus breviceps* (Sugar Glider)

The Sugar Glider was found in a wide variety of habitats, from the Betavip area (200 m) to the upper Sol River Valley (2,300 m). Curiously, we found no evidence of it in the Telefomin and Nong River Valleys (1,500 m) although it was common in the Tifalmin Valley. The animals collected at Ofektaman and the Sol River localities belong to the subspecies *tafa*, and are darker and smaller than animals from lower altitudes. They may yet prove to represent a distinct species.

Because it is small and agile, this species is difficult to hunt, and is probably only rarely consumed (although often heard and seen) by the local people.

### *Dactylopsila trivirgata* (Striped Possum)

The Striped Possum is represented in our collection by two trophy skulls and two young. The young were taken in the Tifalmin Valley (1,400 m), while one of the trophies was purchased at Yapsiei Station and the other at Yominbip. In addition I observed an animal at about 200 m altitude in the Betavip area during spotlighting, but did not collect it. Informants said that this species was common in the Yominbip area, and thus its small size may account for its rarity in trophy collections. The upper altitudinal limit of this species in the study area may be between 1,300 and 1,500 m as there was no evidence of it at Telefomin (1,500 m), the Nong River (1,500 m) or Ofektaman (1,400–1,800m).

### *Dactylopsila megalura* (Great-tailed Triok)

This species is represented in our collections only by the skins of a female and two well-grown young collected at Tifalmin (1,600–1,800 m), and a tail collected at Ofektaman (1,400–1,800 m). All of these specimens were retained as *bilas* by Telefol and Tifal. This species is rare in the study area and probably occurs only above 1,400 m. It is avidly sought after for *bilas*. Telefol informants report that this species exists sympatrically with *D. palpator*. Unfortunately the habits of this species are so incompletely known that the nature of the niche separation that must exist between these species is unknown.

### *Dactylopsila palpator* (Long-fingered Triok)

Only six specimens were collected, two at 1,500 m in the Nong River Valley and four at Tifalmin (about 1,800–2,000 m). However, the species is almost certainly more widespread than this, as informants knew of it from the Sol River Valley and even the Telefomin Valley. Again, this species is prized for use as *bilas*.

## Rodentia

### Muridae

***Hydromys chrysogaster*** (Common Water Rat)

This water rat is widely distributed along the rivers and creeks of the region, up to an altitude of at least 1,000 m. We obtained two specimens in the Betavip area (where it appears to be common) and a single individual (dug out of a burrow) at Yominbip (1,000 m). Telefol informants were familiar with a water rat that inhabits the Telefomin Valley (1,500 m), but we could not determine which species it represented.

***Paraleptomys wilhelmina*** (Short-haired Hydromyine)

A single specimen was caught in a rat trap baited with sweet potato in the Tifalmin Valley at 1,800 m.

***Pogonomys macrourus*** (Chestnut Tree-mouse)

This species seems to be patchily distributed, and where it does occur, is restricted to the altitudinal range about 900 to 1,500 m. It is abundant at Munbil in the Star Mountains (900–1,000 m) where 24 specimens were obtained, and rarer at Yominbip (1,000 m; 2 specimens), the Telefomin Valley (1,400 m; 1 specimen), and the Nong River Valley (1,500 m; 3 specimens). Most animals were obtained by women who dug them out of their burrows, although some were collected at night from trees. Although its lower altitudinal limit in the study area is uncertain (we did little collecting between 400 and 900 m), its upper limit is about 1,500 m, as extensive collecting above this altitude failed to reveal its presence there.

***Pogonomys championi*** (Telefomin Tree-mouse)

*Pogonomys championi* is a small, grey-bellied *Pogonomys*, related to *P. macrurus* or *P. sylvestris*, that has only recently been described (Flannery, 1988). It was encountered at three localities in the study area. Twenty one specimens were obtained at Ofektaman (1,400 m), one individual was caught in the upper Sol River Valley (2,300 m), and many were obtained at Tifalmin (about 1,800 m). Most if not all of the Ofektaman and Tifalmin animals were dug from burrows by women, while the Sol River animal was taken from a tree at night.

***Mallomys rothschildi*** (Black-eared Giant Rat)

This species seems to be relatively common in the primary forest of the Nong River Valley (1,500 m), and at higher altitudes elsewhere along the Central Cordillera. It is represented in our collections by six individuals, two shot at night, three taken from tree hollows and one (a juvenile) from a cave.

*Mallomys rothschildi* is a restricted food to the Telefol, being eaten only by women. This custom is still strongly adhered to. Men will not go out of their way to obtain this species, but if one is incidentally encountered they will attempt to capture it to give to a female family member.

***Mallomys aroaensis*** (Grey Black-eared Giant Rat)

A single subadult male was collected at 1,600 to 1,800 m at Tifalmin — it was shot at night. *Mallomys rothschildi* was captured on the same night by the same hunter.

***Hyomys goliath*** (White-eared Giant Rat)

The White-eared Giant Rat is uncommon in the study area. Only three specimens were obtained: a mother and young at Ofektaman (1,400–1,800 m) and a second female at Tifalmin (about 1,800 m). This species is subject to the same food restrictions as *M. rothschildi* by Telefol.

***Anisomys imitator*** (Uneven-toothed Rat)

A specimen was captured in the upper Sol River Valley (2,300 m) in February 1984, and a second at Tifalmin in 1987. It is probably rare locally and is not a restricted food. Telefol informants indicate that this species is sometimes caught by wrapping a frayed plastic sack around the trunk of a fruiting *Pandanus*. This entangles the animal's hands and feet as it climbs the tree.

***Uromys caudimaculatus*** (Giant Mosaic-tailed Rat)

This is the most common large murid below 1,500 m in the study area. At about 1,500 m both this species and *U. anak* were caught in the Nong River Valley. Among Mianmin the teeth of this species are prized as engravers. In their area it is often caught by waiting in ambush beside a fruiting tree.

***Uromys anak*** (Black-tailed Giant Rat)

A single specimen (a subadult female) was collected in the Nong River Valley in July 1985 and a further two at Tifalmin in 1987. It seems to be rare in the study area, and was not subject to any food taboos.

***Lorentzimys nouhuysii*** (Long-footed Tree-mouse)

This species was common at between 2,000 and

2,600 m in the Sol River Valley, with nine specimens caught, and a further two specimens were taken at Ofektaman. Because of its small size it is probably of little more than snack value to local people. Its main habitat seems to be primary forest, and nests containing several individuals were encountered among epiphytes and between rocks.

### *Xenuromys barbatus* (Giant Rock Rat)

This rare murid is represented in our collections by three whole specimens and six pairs of dentaries. All were collected in the Yapsiei-Betavip and Mount Bubiari areas in January 1984 and April 1986. The three whole specimens were all located in lairs in rockpiles in primary forest at between 400 and 1,300 m altitude. The dentaries of both this species and *U. caudimaculatus* are valued for use as engraving tools. Dogs are often used to locate this species.

### *Pogonomelomys ruemmleri* (Ruemmler's Pogonomelomys)

One specimen of this small murid was collected at 2,600 m in the upper Sol River Valley. It was located it the crown of a *Pandanus*. A second specimen was taken in a rat trap at Dokfuma on the herbfield margin at 3,200 m. This species seems to be restricted to upper montane forest and herbfields in the study area.

### *Pogonomelomys sevia* (Highland Pogonomelomys)

A single individual was collected at Ofektaman (1,400-1,800 m). This represents the westernmost record for this species.

### *Pogonomelomys mayeri* (Shaw Mayer's Pogonomelomys)

A female and two thinly-furred young were collected from the crown of a *Pandanus* in a patch of disturbed forest in the Telefomin Valley at about 1,300 m in April 1986 and a second female from a tree hollow in the Tifalmin Valley (about 1,400 m) in April 1987. All three *Pogonomelomys* species seem to be rare in the study area and are probably of little economic importance to the Ok peoples.

### *Melomys lanosus* (Large-scaled Melomys)

Four specimens were collected in the upper Sol River Valley at 2,300 m, a single specimen at Miptigin (2,000 m) and a further 11 at Tifalmin (about 1,800 m). All were caught in primary mossy forest. This murid is a favoured food item, and its consumption is not subject to food restrictions by Telefol.

### *Melomys rattoides* (Beautiful Melomys)

This species has a very restricted altitudinal distribution, but can be abundant where it occurs. Within the study area we recorded it at 900 m at Munbil (two specimens) and 1,000 m at Yominbip (15 specimens). At Yominbip it was the most commonly caught murid, and was obtained by snap-trapping and the excavation of burrows. Most specimens came from primary forest. The species is greatly favoured as a food item at Yominbip because of its abundance and relatively large size (about 200g). Both the localities that yielded this species are at about 900 to 1,000 m altitude, and extensive trapping at both 200 m and 1,500 m failed to reveal its presence higher or lower. People living at these latter altitudes were unfamiliar with it, and thus it appears to have a patchy and limited distribution.

### *Melomys rubex* (Mountain Melomys)

This species was widespread and common at most localities in excess of 1,000 m and up to 2,800 m. However, it was not found at lower stations. Because of its small size this species is probably of little economic importance.

### *Melomys* sp.

Six specimens of a large, dark coloured *Melomys* were trapped near the margin of the Dokfuma herbfield (3,200 m), most in relatively open situations. Although close to *M. rubex* in cranial morphology, their status is currently uncertain.

### *Melomys rufescens* (Black-tailed Melomys)

This species was encountered at most collecting stations at altitudes below 1,500 m, and was most often found in very disturbed environments. Indeed, it was often captured in village environs, even living in the thatch roofs of huts. It is common in the extensive grasslands of the Telefomin Valley. However, we obtained no records from primary forest. Curiously, it did not appear to be looked upon with enthusiasm as a food item.

### *Melomys platyops* (Lowland Melomys)

This species was encountered only below about 300 m in the study area. There, however, it was common. It is certainly not present at altitudes in excess of 1,000 m, as extensive work there failed to reveal its presence. It was present in both primary and disturbed habitats.

***Rattus niobe arrogans*** (Moss Forest Rat)

Nineteen individuals of this distinctive taxon were taken in rat traps set in the subalpine herbfield at Dokfuma, Star Mountains at 3,200 m. Its heavier weight, (R = 45–59, M = 50.0, N = 14 as opposed to R = 34.5–50, M = 42.3, N = 9) and more rufescent colouration make it readily distinguishable from *R. n. pococki*.

***Rattus niobe pococki*** (Moss Forest Rat)

Specimens of this small and very black subspecies of *R. niobe* were taken at 1,800 m at Tifalmin, and between 2,300 and 2,600 m in the Sol River Valley. This taxon appears to be uniform in morphology throughout its altitudinal range, and I could find no evidence of it intergrading into *R. n. arrogans*. Indeed, *R. n. arrogans* probably replaces *R. n. pococki* at between 2,600 and 3,200 m in the study area. This distribution pattern is more suggestive of species than subspecies, and it is likely that future study will show that these two taxa are distinct species.

***Rattus*** sp. cf ***R. niobe***

Three specimens of a *Rattus niobe*-like species were collected (2 at Yominbip, 1,000 m and 1 at Ofektaman 1,400 m). The fur is slightly spinous, the tail uniformly black, and the molars small and relatively simple. The molars in particular are reminiscent of *Rattus praetor*. However, based on dental wear and the proportions of the hindfoot, the specimens are not juvenile *R. praetor*. These rats are just slightly larger than *R. n. arrogans* (head-body length = 126.8–138.8, N = 2 as opposed to 99–120, N = 14). Further revision of the small *Rattus* species of montane New Guinea is clearly necessary.

***Rattus verecundus*** (Slender Rat)

A single specimen of this species, similar in morphology to the subspecies *unicolour*, was trapped at 2,600 m in the Sol River Valley in April 1986.

***Rattus steini*** (Small Spiny Rat)

This is by far the most abundant murid in the study area, and was collected at most stations from 120 to 2,300 m. It was usually trapped in disturbed habitats, and in some areas (e.g. grassland around Telefomin, gardens at Munbil), it was present in plague proportions. However, it was rarely trapped in primary forest.

In the past this species was often eaten by women, but at least among Telefol this practice is falling into disuse, possibly because the rats are foul smelling and display what the Telefol consider to be disgusting habits, and because store bought protein is readily available.

***Rattus praetor*** (Large Spiny Rat)

This species was encountered at Munbil (900 m), and the Yapsiei/Betavip area (200–300 m), where it exists sympatrically with *R. steini*. Both *R. steini* and *R. praetor* seem to be regularly encountered by women while gardening. This species is difficult to distinguish from *R. steini* in the field, and these species are not differentiated in the Atbal and Mian languages.

## Megachiroptera

### Pteropodidae

***Rousettus amplexicaudatus*** (Rousette Bat)

This species was only encountered in the Yapsiei-Betavip area (200–300 m), where it was very common. Extensive mistnetting failed to reveal its presence at higher altitudes. It appears to breed seasonally in the Yapsiei area, with births in February-March (Flannery, 1990). Despite its abundance, this species is difficult to obtain by any method except mistnetting, and so is rarely obtained by Mianmin.

***Pteropus neohibernicus*** (Greater Flying Fox)

This is the largest of the New Guinean Chiroptera, and as such is a desirable prey item. By day it forms large camps in swampy parts of the August-Sepik floodplain. At night the bats disperse into the foothill forest to altitudes up to 1,000 m. During January 1984 these bats were commonly seen in hill forest in the Yapsiei-Betavip area, but they were not observed in this area in April 1986. Their abundance is doubtless related to the fruiting of forest trees, and thus they are probably an intermittently available food source.

***Dobsonia moluccensis*** (Bare-backed Fruit Bat)

The Bare-backed Fruit Bat was found at virtually all localities visited, except the upper Sol River Valley. Large congregations of this species exist in caves in the valley of the Nong River, and doubtless it is common in other suitable caves in the region. Because it can be found in large numbers and can be readily harvested, Telefol and Mianmin will travel considerable distances to the caves where it exists to trap it. Hundreds of animals are often captured, which must contribute considerably to the diet of the local people at such times. The roosts of this species on Mount Bubiari receive partial protection from a Mianmin belief that the discharging of shotguns in the

caverns inhabited by the bats will incur the displeasure of spirits.

***Dobsonia minor*** (Lesser Bare-backed Fruit Bat)

The altitudinal distribution of this species coincides with that of *Rousettus amplexicaudatus*, being collected only in the Yapsiei-Betavip area below 300 m. It is less common than *R. amplexicaudatus*, however, and seems to be most often caught in mistnets set along overgrown creeks.

***Nyctimene cyclotis*** (Round-eared Tube-nosed Bat)

A single specimen belonging to the subspecies *M. c. certans* was taken at 2,300 m in a mistnet set in a garden in the upper Sol River Valley. This species may represent the Telefol folk taxon *Brulim*. *Brulim* is held in great superstitious dread by most Telefol. It is considered extremely ill fortune to kill one, it being widely accepted that the hunter will die within 48 hours of such an act. Because of this it was not possible to check the species identification with Telefol informants. However, in most particulars this species fitted descriptions of *Brulim* given by several Telefol.

***Nyctimene albiventer*** (Common Tube-nosed Bat)

This species was abundant at all collecting stations from 120 m to 1,000 m. However, it was not taken at stations above this altitude, even though intensive netting was carried out there. The specimens collected by us are highly variable, and more than one biological species may be involved. This and the other small, non-cave dwelling bats of the region are probably of little economic importance to the Ok peoples as they are not readily captured using traditional techniques.

***Nyctimene aello*** (Greater Tube-nosed Bat)

Four specimens were taken in the Yapsiei-Betavip area during April 1986. All three females were lactating. As with *Rousettus amplexicaudatus* and *Dobsonia minor*, this species does not seem to occur at altitudes higher than about 300 m in the study area.

***Paranyctimene raptor*** (Unstriped Tube-nosed Bat)

This species was common at Betavip (200 m, 7 specimens) and present at Munbil (900 m, 3 specimens) but was not taken at Yominbip (1,000 m) or localities at higher altitudes.

***Macroglossus minimus*** (Northern Blossom Bat)

This blossom bat was commonly caught at collecting stations at altitudes from 160 to 1,000 m, and was as common relative to *Syconycteris australis* at higher as at lower stations. It was usually about one sixth as common as *S. australis* (Betavip area 200 m 5.5:1, Munbil 900 m 6.3:1, Yominbip 1000 m 2.3:1). Zeigler (1982) reports that elsewhere in New Guinea it is much more common relative to *S. australis* at 200 m than at 1,000 m.

***Syconycteris hobbit*** (Moss Forest Blossom Bat)

A single specimen was taken at 2,300 m in the upper Sol River Valley. This species was previously known only from Mount Kaindi, Morobe Province (Zeigler, 1982). At both localities it is sympatric with *S. australis*.

***Syconycteris australis*** (Common Blossom Bat)

This was the most widespread and abundantly-caught mammal during our study. However, all specimens were taken from mistnets, and the species is only rarely captured by Ok peoples. It was present at all collecting stations where mistnets were erected, except at Dokfuma (3,200 m) with up to ten specimens being taken per night. Some variation with altitude was noticed, with specimens from higher altitudes being more sombre in colouration.

## Microchiroptera

### Vespertilionidae

***Nyctophilus microtis*** (Small-eared Nyctophilus)

Two specimens (one of which escaped) were trapped in mistnets set in a clearing in primary forest near Betavip (200 m).

***Pipistrellus collinus*** (Mountain Pipistrelle)

A single individual was taken in a mistnet set in a garden in the upper Sol River Valley (2,300 m).

***Kerivoula muscina*** (Fly River Trumpet-eared Bat)

Three individuals were taken from a rolled banana leaf at 1,600 m at Tifalmin. Others were present but escaped.

***Miniopterus australis*** (Little Bentwinged Bat)

Twelve specimens were obtained in a cave situated

approximately 1 km north-west of the northern end of the Telefomin airstrip (1,500 m). The cave was large, open, and easy of access. *Miniopterus macrocneme* was also present. All cavernicolous bats whose colonies are accessible are harvested by Telefol and Tifal for food.

***Miniopterus*** sp.

A single specimen of a large *Miniopterus macrocneme*-like species was taken in a mistnet at 3,200 m in the Star Mountains at Dokfuma. The forearm is larger than typical *macrocneme* from lower altitudes (see Table 6) and for this reason it is treated separately here.

***Miniopterus macrocneme*** (Small Melanesian Bentwinged Bat)

This is the most abundant and widespread of the *Miniopterus* species in the study area. It was encountered in numerous caves, ranging in altitude from 1,400 to 2,600 m. The caves were usually large and relatively open, and were often dry. A sandstone cleft containing only this species was located at 2,600 m near the head of the Sol River Valley. Much of the cleft was in the twilight zone, and when visited in the late morning the bats were torpid. Torpid bats were also located in a large cave in the Nong River Valley at 1,500 m. Caves sheltering *M. macrocneme* were in one case also home to *M. australis*, and in another to *M. magnater*.

***Miniopterus medius*** (Javan Bentwinged Bat)

A single specimen of a bat similar in size to that reported as *M. medius* from the Wau area by Hill (1983) was found roosting in a shallow limestone cave at 1,340 m near Tifalmin. The same cave also sheltered *Hipposideros cervinus* and *Emballonura beccarii*. A small solution tube at the end of the cave was the only area out of the twilight zone. Measurements for the *M. medius* specimen are given in Table 6.

***Miniopterus magnater*** (Western Bentwinged Bat)

Eleven specimens of this large *Miniopterus* were found roosting in large caves in the Nong River Valley and Miptigin ridge (1,500 m and 2,000 m respectively). In one case the caves were shared with the more abundant *M. macrocneme*. Measurements are given in Table 6.

## Hipposideridae

***Hipposideros ater*** (Dusky Horseshoe Bat)

A single specimen was taken from a limestone cave at about 1,600 m on the hill south of Tifalmin in April 1987.

***Hipposideros corynophyllus*** (Telefomin Horseshoe Bat)

This species was known previously from a single specimen collected near Telefomin. In July 1985 T.F. Flannery collected a second specimen in the Nong River Valley, which was roosting in a limestone cave with *H. wollastoni* at 1,500 m. During our survey of the Tifalmin area in April 1987 this species was found to be common in caves on hills both to the north and south of Tifalmin, between 1,600 m and 1,800 m. It was often found in association with *H. wollastoni*.

***Hipposideros wollastoni*** (Wollaston's Horseshoe Bat)

This species is widespread and common in the survey area. We encountered it at Telefomin (1,400 m), the Nong River Valley (1,500 m), Miptigin ridge (2,000 m), and Tifalmin at (1,600–1,800 m). It was usually encountered in the deeper and wetter caves, which it often shared with *H. corynophyllus*. Drier and more open caves were usually inhabited by species of *Miniopterus* and *Emballonura*.

***Hipposideros cervinus*** (Fawn Horseshoe Bat)

Only four specimens of this species were taken during our survey. Three were found in a shallow cave at 1,340 m near Tifalmin, while a third was taken in a mistnet set in a clearing in primary forest near Betavip at 200 m.

***Hipposideros diadema*** (Diadem Horseshoe Bat)

A single specimen was shot with a bow and arrow while it was roosting in a low tree near the August River, half way between Yapsiei and Betavip (altitude 200 m), in January 1984.

## Rhinolophidae

***Rhinolophus arcuatus*** (Western Horseshoe Bat)

A single specimen was taken from a cave to the north of Tifalmin at about 1,500 m and a further four from west of Tifalmin. The Australian Museum also holds nine specimens collected in 1956 by D. McMichael, at a cave 1.6 km north of Telefomin. These had previously been misidentified as *R. megaphyllus*. It is probable that they are from the same cave (or a nearby one) as the type specimens of *R. a. mcintyrei* Hill & Schlitter, 1986.

### Emballonuridae

***Emballonura beccarii*** (Beccari's Sheathtail Bat)

Twenty four individuals were taken from a limestone cave situated at about 1,300 m on the south side of the Sepik River south of Bogalmin in May 1986. A further six specimens were collected in a cave at 1,340 m near Tifalmin in April 1987. Both males and females were represented in both of these collections.

***Emballonura raffrayana*** (Raffray's Sheathtail Bat)

Two colonies were located, one in a shallow limestone cave on the north side of the Sepik River south of Telefolip at 1,280 m, and the second in a partially collapsed shale overhang near Yominbip at 900 m. At Telefomin only males (10) were caught while at Yominbip both males and females (16) were taken. Both caves were small and shallow, and were inhabited only by *E. raffrayana.*

***Emballonura nigrescens*** (Lesser Sheathtail Bat)

This species was encountered both in the Yapsiei/ Betavip area, where it was commonly taken in mistnets at dusk, and at Yominbip, where a colony of six were found roosting on the underside of a leaf in a large tree left standing in a garden. It was often active around villages just before and at dusk, and the Mianmin name (Heba-Heba) means 'crowded together', a reference to its roosting habit.

## Introduced Mammals

***Sus scrofa*** (Pig)

Wild pigs are common at lower altitudes within the study area. They are abundant on the Yapsiei/Sepik floodplain, and in parts there is considerable disturbance to the forest understorey. At higher altitudes, however, wild pigs become less common. They are extremely rare if present at all in the Telefomin and Tifalmin Valleys, and curiously, are absent altogether in the subalpine grasslands of the Star Mountains. Similar grasslands on Mount Albert Edward, Central Province, support a large feral pig population (personal observation). The domestic pig population in the study area is not large compared to that sometimes seen in the central highlands, possibly due to the relatively small amount of sweet potato cultivation undertaken in the area. However, locally around villages in the Yapsiei area and in the Telefomin valley, understorey disturbance by domestic pigs can be severe.

***Canis familiaris*** (Dog)

The only wild dog population encountered by us was in the subalpine grasslands at Dokfuma. Here dogs seemed plentiful, and Wopkaimin report taking puppies and domesticating them. Domestic dogs are present in most human communities. They are often used for hunting.

***Felis catus*** (Cat)

Domestic and probably wild cats are present in the Telefomin Valley, but do not seem to be common. The spread of cats into more outlying settlements is still continuing, and we had the opportunity to do extensive fieldwork in Betavip Village both before and after the introduction of domestic cats. During 1984, extensive trapping and hunting was carried out around Betavip. When the area was again visited in 1986, a similar program was instituted. In the intervening period two cats had been introduced to Betavip, and some of the faunal differences that we observed are probably related to this. Changes included a drastic decline in the number of spiny bandicoots (*Echymipera* spp.) encountered (see species accounts), as well as a decline in *Rattus steini* and *Rattus praetor* in the immediate village environs. When questioned, Mianmin were well aware of these changes, and attributed them to the cats. The decline in *Rattus* numbers was applauded by the Mianmin, while the loss of bandicoots was regretted as they represented a valuable food resource. Elsewhere cats have been the cause of extinction of several small vertebrates (Diamond, 1982).

### Muridae

Only one introduced murid species, *Mus musculus* (House Mouse), was encountered in the study area. It was abundant around settlements and particularly in stores in the Telefomin Valley, but was not seen elsewhere. Both *Rattus exulans* and *Rattus rattus* are unknown in the region, although *Rattus rattus* were obtained around gardens and houses at Bultem village near Tabubil, to the south of the study area. The absence of *Rattus exulans* is remarkable, as it seems to have penetrated into most other areas of human habitation within New Guinea.

***Bos taurus*** (Cattle)

A few cattle exist in the vicinity of Telefomin Station. They are confined to anthropogenic grassland, and are in poor condition.

## Discussion

**Comprehensiveness of survey and comparison with 3rd Archbold Expedition.** Our survey consisted of over six months in the field, with party size varying from

two to six. Although every effort was made to sample in all habitat types in the region, and mammal sampling was our primary goal, it is clear that many species that probably inhabit the region eluded us. Evidence that species exist in the area that we did not encounter comes from four major sources: 1) results of previous expeditions in the area; 2) comparisons with the results of the 3rd Archbold Expedition to the Mount Wilhelmina area, Irian Jaya; 3) folk taxonomies collected from Telefol and Mianmin, and 4) an analysis of known species distributions.

**Previous collections.** The only previous collections from our study area that include species not taken by us are those made by Abid Beg Mirza and others for the Bishop Museum, Hawaii in 1970 to 1971 and material collected by Dr D. Hyndman and reported upon by Hyndman & Menzies (1980). The British Museum collections include *Macruromys major* (one from Telefomin at 1,500 m), *Mayermys ellermani* (with one specimen taken at Feramin, 8 km south-east of Telefomin at 1,400 m), *Neohydromys fuscus* (at least one specimen from Lake Louise at 2,600 m), *Micromyonomys richardsoni* (one from Telefomin at 1,500 m) and *Pseudohydromys occidentalis* (Lake Louise, 2,600 and 2,800 m).

The Hyndman material includes the only non-fossil remains of *Aproteles bulmerae* known. Although searched for by us at its previously known haunt, no animals were encountered.

**Comparisons with 3rd Archbold Expedition.** The 3rd Archbold Expedition is the only major mammal survey, apart from our own, to have been carried out over a broad transect on the northern slopes of the New Guinean Central Cordillera. They worked extensively in the Idenburg River — Lake Habbema area in 1938–1939 (Archbold, Rand & Brass, 1942), covering a similar altitudinal transect to us. This area lies 300 to 400 km to the west of our study area, but nonetheless is topographically and faunistically very similar to ours. Indeed, many taxa are shared between these two locations that are not found to the east of our study site. For this reason, it is valuable to compare the results of the two expeditions, as combined the results give a greater understanding of mammal diversity and distribution than the results of one expedition viewed in isolation.

Table 7 lists mammal species recorded by us as well as those from the 3rd Archbold Expedition. The latter list is compiled from the works of Tate (1941, 1942, 1945a,b, 1947, 1948a,b, 1951), and Archbold, Rand & Brass (1942), with some changes made by later systematic reviewers. The altitudinal range that the taxon was encountered within is also given. As can be seen, where a taxon was taken by both expeditions in reasonable numbers, there is usually a good concordance in the altitudinal range that it was located over in both areas. This would suggest that altitudinal zonation is similar at both locations. A more intriguing aspect, however, is the species taken during only one or the other survey. These differences in the species collected can probably be accounted for by two major factors; sampling techniques, and faunal differences. Some absences, however, are not easily accounted for by either factor.

**Taxon absences due to sampling.** It is clear from Table 7 that the collections made by us are depauperate in small insectivores/carnivores compared with those of the 3rd Archbold Expedition. Indeed, five species of dasyurid and four species of hydromyine murid which were collected by the Archbold expedition (often in abundance) are not represented in our collections. Almost all of these species are widespread in western New Guinea, and indeed, descriptions matching some of these species were obtained from local people in our study area or have been collected there by others. Their absence in our collections therefore is almost certainly due to the limited trapping with protein- rich baits that we undertook. Conversely, the very few smaller megachiropteran and microchiropteran bats obtained during the 3rd Archbold Expedition in all likelihood reflects their limited use of nets, and absence of work in caves. The 3rd Archbold expedition also failed to locate any *Dendrolagus* spp, *Thylogale brunii*, *Phalanger matanim*, *P. vestitus*, *Dactylopsila trivirgata*, and *D. megalura*. Their relations with local peoples seem generally to have been poor, and many of these species were procured for us only by local helpers. It may well be that the lack of some of these species in their collections and their lack of work in caves (to locate caves in our study area almost always required local expertise) was due to a lack of rapport with local landowners. It is also possible, however, that some of these species (e.g. *Thylogale brunii* and *Dendrolagus dorianus*) are extinct in much of Irian Jaya (see Hope, 1976).

**Taxon absences due to faunal differences.** Several species collected during the 3rd Archbold Expedition in Irian Jaya may simply not exist in our study area. These include *Phascolosorex doriae* (which has never been reported east of the Idenburg River, but is abundant to the west), *Rattus richardsoni* and *Melomys albidens*. These latter two species occur only high in the subalpine and alpine grasslands of the Snow Mountains. Such habitat is very restricted in our study area, and the alpine grasslands of Irian Jaya are well separated from such habitats in Papua New Guinea, making dispersal of species closely tied to alpine grassland habitats difficult. Thus, it may be that these species do not inhabit the limited subalpine areas of the Star Mountains.

Conversely, it appears likely that several species collected by us do not occur in the Snow Mountains/ Idenburg River area. These include *Dendrolagus goodfellowi* (which has not been recorded west of Mount Bubiari, West Sepik Province; this work), *Pogonomelomys sevia* (which has not been recorded west of Telefomin), and the large grey *Melomys* close to *Melomys rubex*, which is known only from Mount Capella. None of these species have ever been recorded from Irian Jaya, and are either common (*Melomys* sp.) or obvious

(*D. goodfellowi*) where they do occur.

**Differences of uncertain cause.** Several differences between the collections of the 3rd Archbold Expedition and our own work are not readily explained by any of the above causes. These include the absence of *Petaurus breviceps* and *Pseudocheirus forbesi* from the Archbold collections, and the absence of *Melomys lutillus* from ours. *Petaurus breviceps* seems to be abundant and widespread throughout most habitats in New Guinea. It is difficult to believe that it is absent from the area traversed by the 3rd Archbold Expedition. However, it is equally difficult to believe that if it had been present in anything like its abundance elsewhere, that specimens would not have been obtained by Expedition members.

The situation with *Pseudocheirus forbesi* is even more intriguing, for this species is the most abundant pseudocheirid in our study area. It is found in primary forest and secondary growth throughout our study area between 1,400 and 2,300 m. Although the Archbold Expedition obtained all the other pseudocheirid species obtained by us, as well as one species that we did not collect, they did not obtain a single *P. forbesi*. *Pseudocheirus forbesi* is known from the Vogelkop; thus if it is absent in the Snow Mountains/Idenburg River area, this must represent a gap in its distribution. If such a gap exists, it would represent a truly intriguing zoogeographic problem.

Almost as peculiar is the absence of *Melomys lutillus* from our study area. The Archbold Expedition found this species to be abundant in the Baliem Valley. However, extensive trapping shows that it is absent in the Telfomin and the other grassy valleys in our study area. This species is extremely widespread elsewhere in Papua New Guinea, so its apparent absence from the Telefomin area is not readily explained.

**Folk taxonomy.** Folk taxonomies collected from Mianmin and Telefol include several names for taxa that we did not obtain during our survey. Some taxa were well-enough described that we feel confident that we can identify them. These taxa are as follows: *Hom* (Mianmin) = *Myoictis melas*; *Tning* (Telefol) = *Neophascogale lorentzi*; *Bilbilok* (Telefol) = *Parahydromys asper*; *Dikrus* (Telefol) = molossid bat. All of these taxa were widely recognised among the inhabitants of the study area. Our failure to trap them doubtless stems from the same factors discussed previously.

**Analysis of species distributions.** Several species have not been recorded in the study area, but may nonetheless occur within it. This applies in particular to such hard to obtain taxa as molossid bats and tree-roosting vespertilionids. Some of these taxa occur to both the east and west of our study area or extremely close to it, but have not yet been recorded from within it. We regard it as highly likely that these taxa do indeed occur within our study area but they are sufficiently rare or difficult to catch that they were missed by our survey. These species include *Antechinus wilhelmina*, *Murexia longicaudata*, *Phascolosorex dorsalis*, *Neophascogale lorentzi*, *Myoictis melas*, *Pseudocheirus canescens*, *Emballonura furax*, *Hipposideros calcaratus*, *Aselliscus tricuspidatus*, *Rhinolophus megaphyllus*, *R. euryotis*, *Phoniscus papuensis*, *Myotis adversus*, *Pipistrellus papuanus*, *P. angulatus*, *Murina florium*, *Miniopterus schreibersi*, *Chaerephon jobensis*, *Mormopterus beccarii*, *Hydromys habbema*, *H. hussoni*, *Crossomys moncktoni* and *Parahydromys asper*.

A number of other microchiropteran species, while currently known only from eastwards of the study area, may well also occur within it, as their absence from western New Guinea is probably due to the paucity of chiropteran survey work done there. These species include *Philetor brachypterus*, *Tadarida kuboriensis*, *Otomops papuensis* and *O. secundus*.

**Faunal diversity.** Thus our list includes 23 species which could confidently be expected to occur in our study area (on the basis of folk taxonomy or distribution), and a further four poorly known chiropteran species which may occur within it. Thus, in addition to the 87 taxa encountered during our survey and six collected by others, a further 27 taxa may exist in the region. Some of these 27 almost certainly do exist there, while others are more doubtful. Thus the total diversity of indigenous mammals in this region lies somewhere between 93 and 120 mammal species, and more probably near the upper value. This is an astounding total for such a small region, and is, as far as we know, the highest recorded mammal diversity for a similar sized area in the Australasian region. Indeed, it rivals the 145 land mammal species reported for Suriname, a much larger area in the Neotropics (Husson, 1978). Unfortunately, few comparable mammal surveys have been completed in Papua New Guinea, but as a comparison, the work of Hide *et al.* (1984) and Dwyer (1983) can be examined. Hide *et al.* (1984) is a survey of part of the South Chimbu (about 2,997 km$^2$), at altitudes ranging between 400 to 2,569 m. It yielded only 59 species, which is low even considering that Microchiroptera were poorly sampled. Dwyer (1983) records only 44 species in his survey of the mammals of Mount Elimbari (at altitudes of 1,900 to 2,730 m), Chimbu Province. Interestingly, Beehler *et al.* (1986) note that the upper Sepik is one of the areas of greatest bird diversity in New Guinea, with 165 to 170 resident forest species being present. Thus, our study area may indeed be a region of exceptional biotic diversity, although further research on other groups is needed before this can be confirmed.

The factors that gave rise to and sustain the diversity of mammals in our study area almost certainly include the following: 1) *altitudinal range*. The study area encompasses habitats at altitudes from 120 to 4015 m. Of these we sampled from between 160 to 3,200 m, which ranged from lowlands jungle developed on floodplain, to subalpine herbfield. This range encompasses most of the major habitat types to be found on mainland New Guinea; 2) *local climatic variation*. Although weather patterns are still poorly understood, it is apparent that

rainfall varies markedly throughout the region. Included are some of the wettest regions in New Guinea, but some of the valleys in the middle altitudes seem to lie in rainshadows. This has a dramatic affect on forest composition and structure, and probably upon mammal diversity; 3) *location.* The study area is located almost in the geographic centre of the island of New Guinea. Some species with a predominantly western distribution reach their easternmost limit in the study area, while others with an eastern distribution find their westernmost limit there; 4) *low human population.* The entire region supports only around 10,000 people. Their impact on many areas is as yet slight, and thus some important mid-altitude forests have not suffered degradation and are capable of supporting a diverse mammal fauna. Furthermore, in the more elevated areas pig numbers are low and their damage is correspondingly slight, and other introduced species are not common.

**Zoogeography.** *Endemism and zoogeographic patterns.* Our study area encompasses the habitat of three species (*Phalanger matanim*, *Pogonomys championi* and *Hipposideros corynophyllus*) that are known as fossil or living animals from nowhere else, and a further four species (*Dactylopsila megalura*, *Paraleptomys wilhelmina*, *Melomys lanosus* and *Hipposideros wollastoni*) which are found only along the Central Cordillera to the west of Telefomin. A further species, *Rhinolophus arcuatus*, although previously known only from the Telefomin area in New Guinea, is now represented by specimens held in the Australian Museum from Southern Highlands Province. A further species, *Pseudohydromys occidentalis*, also has a 'western' distribution. However, it is differentiated from *P. murinus* from eastern New Guinea only on the basis of size, and the relationship between these species is more similar to that between the western and eastern subspecies of *P. sericeus*, *M. longicauda*, and *D. dorianus* rather than the other western endemics which have no eastern counterparts.

The altitudinal zone occupied by these seven 'endemic and western' species is intriguing, for they are not found in the disjunct upper montane forest, but instead are largely restricted to the midaltitude Oak Forest zone. Within the study area the altitudinal range of this zone varies with local topography, but usually lies between 1,500 to 2,000 m. Table 8 lists the endemic species and their altitudinal ranges. This concentration of endemism seems all the more unusual when one considers the fauna of the upper montane zone. For there, although there are often eastern and western New Guinean subspecies pairs (e.g. in *Phalanger sericeus*, *Dendrolagus dorianus*, *Microperoryctes longicauda*), or species pairs (*Pseudohydromys occidentalis/murinus*), there are no species for which ecological vicars do not exist in the east. In the Snow Mountains in central Irian Jaya, however endemic species are found for which there are no obvious vicars elsewhere (e.g. *Rattus richardsoni*, *Melomys albidens*).

In summary then, the overall pattern is that of a ubiquitous lowland fauna (at least north of the Central Cordillera), a midmontane fauna with a significant and diverse endemic or 'western' element which has no eastern counterpart, and an upper montane fauna with many western distributed species or subspecies, all of which have ecological counterparts in the east. The historical factors that could have produced such a pattern are not immediately apparent. The division of the upper montane zone that led to the development of eastern and western subspecies may well be related to the low point on the Central Cordillera that is situated just to the east of our study area (4°55'S, 131°45'E). Here, the top of the Central Cordillera dips to 1,560 m and drops rapidly into the valleys of the Ok Om (south) and the Hak (north). This region has not been examined zoologically, but it seems likely that today it acts as a barrier to the fauna of the upper montane zone. However, 18,000 years ago, when altitudinal zones were markedly depressed and the tree line was at about 2,100 m (Hope & Hope, 1976), the upper montane zone may well have been continuous across it.

The origin of midmontane endemism in Western New Guinea appears to predate the terminal Pleistocene as the distinctiveness of the taxa involved is greater than that of those of the upper montane zone. Their presence implies two major problems: the origin of the endemics and the factors preventing their spread into apparently suitable habitats in eastern New Guinea.

A possible answer to the problem of origin may lie in the tectonic history of New Guinea. Throughout most of the Miocene, the Central Cordillera of New Guinea was an island archipelago. A fundamental and long lasting marine barrier persisted throughout this time a little to the east of present day Telefomin (Flannery, 1990). This area corresponds with the eastern limit of distribution of the endemic species under discussion.

It seems likely that species that formed the original biota of the islands of the Miocene west New Guinean archipelago may have included taxa ancestral to the species that are endemic to that area at present. But why should these species be concentrated in the midmontane zone?

Climatic regimes were clearly quite different in the Australasian region in Miocene times to those that exist at present (Barlow, 1981). It is clear that throughout the Tertiary high mountain ranges have never linked the New Guinean Central Cordillera and eastern Australia (Dow, 1977), and yet somehow species which are extremely poor dispersalists and which are restricted to cool environments and are of Gondwanian origin (e.g. *Nothofagus* spp.) exist in montane New Guinea. At present many such plant taxa are restricted to areas above 900 m (Hartley, 1986), but in the past these data suggest that they must have existed at lower altitudes. With this in mind, it seems probable that climatic change has forced an upwards migration of these Miocene biotas in the New Guinean montane region. Thus it is possible that the fauna and flora characteristic of the midmontane zone at present may have been related to the dominant biota on the Miocene western islands of New Guinea, even near sea level, and that subsequent climatic changes restricted

it to its present altitudes. An alternative explanation of this phenomenon may be that competition with new immigrants from Malesia restricted the original flora and its associated fauna to the midmontane zone, as the majority of low altitude plants found in Papua New Guinea today are of Malesian origin (Hartley, 1986).

The reason as to why these midmontane endemic elements have not spread to the east is not easily understood. They include bats, murids and marsupials — a range of taxa with a presumably wide range of dispersal abilities. Furthermore, no gaps in the midmontane zone have been identified that would retard dispersal. Overall floristic richness also does not seem to be a factor, as Hope (personal communication) suggests that the flora of Irian Jaya and the Telefomin area is, if anything, less diverse than that of the rest of Papua New Guinea. Clearly some factors are at work that we do not understand, and only further research on the biology and ecology of these taxa will provide answers.

A second major area of zoogeographic interest in this region is the species that reach their westernmost limit in the area. Only two species clearly fall into this category, *Dendrolagus goodfellowi* and *Pogonomelomys sevia*. Others, such as *Syconycteris hobbit*, may do so but their ranges are so poorly known at present that such a designation would be premature. The distribution of *D. goodfellowi* is unusual in the study area as it does not inhabit the Central Cordillera proper, but rather the outlying foothills and ranges to the north of the Sepik. It reaches a natural western limit to its distribution at Mount Bubiari, which is the last outlier reaching over 1,000 m before the Sepik begins its vast curve back to the east (Fig.2). This suggests that the formation of the Sepik drainage predates the evolution of *D. goodfellowi*, otherwise this species would probably be found on both sides of the river. The reason that *D. goodfellowi* is not found to the south of the Sepik, however, is not so apparent. Forests suitable to support it must be found in the upper Sepik drainage. Why it has not managed to use these forests as a bridge to infiltrate the extensive midmontane forests to the south of the Sepik remains mysterious.

The distribution of *Pogonomelomys sevia* is less well understood. Its westernmost limit is apparently the Telefomin valley where it is rare, although to the east it can be common in the mid to upper montane forests. There appear to be no ecological vicars for it to the west, and no barriers to its dispersal in that direction either. An explanation for this distribution must await further study.

**Human effects on mammals.** Through hunting, burning and gardening, humans have a great effect on wild mammals in the study area. The effects of hunting are quite different from that of burning and gardening, which are sometimes associated, so the human impact will be dealt within two parts.

*Hunting*. Those species most affected by hunting in the study area are the large mammals. These include both *Dendrolagus* species, *Zaglossus bruijnii* and possibly *Thylogale brunii*. A further species severely affected is the bat *Aproteles bulmerae*. Both *Aproteles bulmerae* and *Zaglossus bruijnii* have suffered drastic declines in the study area in recent times. Before the 1960's *Zaglossus bruijnii* seems to have been relatively common in the vicinity of Telefomin Station. It was protected by tradition, and thus was not hunted. As traditional beliefs broke down under missionary influence, the species became rarer, so that today it is almost unknown in the region of the station. The rapid extinction of this species in some areas of the central highlands reported upon by George (1978) may soon follow in much of the Telefomin area if some protection is not again granted.

Parallels between *Aproteles bulmerae* and *Zaglossus bruijnii* are remarkable. For *A. bulmerae* has also become extinct in the highlands, albeit in prehistoric times (Menzies, 1977). A single colony was located in our study area by D. Hyndman in 1975. It occupied a deep doline which was extremely difficult to access, called Luplupwintem on the Finimterr Plateau. The colony doubtless survived because of the inaccessibility of its main roost. Unfortunately, Finimterr is crossed by a track leading from Tifalmin to Bultem. With the development of the Ok Tedi Mine, this path began to receive frequent traffic. Shotguns also became more widespread. This combination proved fatal to the Luplupwintem colony. The cave has been checked on several occasions for bats, but none have been seen since 1977, when two were observed circling the roost. Conversations with Wopkaimin hunters indicate that literally hundreds of animals were shot at a time when one shotgun was taken into the cave in the mid 1970's.

In both the case of *A. bulmerae* and *Z. bruijnii* it seems that the delicate balance between these species and humans has been upset with the coming of European ideas and technology. If both species still exist in the study area, their continued existence is probably tenuous. More research and government action is necessary to ensure their safety.

*Dendrolagus dorianus*, *D. goodfellowi* and possibly *T. brunii* have suffered some local extinction, but are still secure in at least part of the study area. Although probably hunted to extinction in parts of the Telefomin area, *D. dorianus* is still common in the more remote parts of the Star Mountains. It should remain secure there for the foreseeable future. Likewise, *D. goodfellowi* has probably been adversely affected in some of the outlying parts of its range around Yapsiei, but is apparently secure on the higher slopes of the Thurnwald Range. The status of *T. brunii* is uncertain. Elsewhere in Papua New Guinea it is common. However, in our study area it is rare. This may be due to hunting and clearance at middle altitudes, or it may be natural.

*Burning and gardening*. Burning, gardening and the building of dwellings has had a beneficial effect of some species, and a detrimental effect on others. Species capable of utilising disturbed habitats, such as *Echymipera rufescens*, *E. kalubu*, *Rattus praetor*, *R. steini* and *Melomys rufescens* can be abundant around villages, in gardens, and even in anthropogenic grasslands near the larger settlements. Indeed, some species such as

*E. rufescens* may depend upon human maintained habitats for their existence in the study area.

Gardening and burning have, however, destroyed considerable amounts of primary forest, particularly in the Telefomin and Tifalmin areas. Here, anthropogenic grassland now occupies large tracts once covered by primary midmontane forest. Midmontane forest between 1,500 and 2,500 m, particularly the lower Oak zone, supports the largest diversity of mammals of any habitat in the study area. Indeed, seven species which are not found elsewhere in Papua New Guinea are confined to this zone. Figure 9 shows the approximate extent of the 1,500 to 2,500 m zone, and the parts of it that have been disturbed by human activity. Much of this disturbed area is now either anthropogenic grassland, early secondary growth, or gardens. Although there appears to be no immediate danger to the endemic midmontane mammals from gardening and burning, such a threat could arise if the human population undergoes an increase.

**Conservation priorities.** Conservation initiatives are urgently needed in three different areas in order to maintain the exceptionally rich mammalian assemblage currently found in the study area. These are as follows: *Preservation of Aproteles bulmerae*. The only living individuals of this endemic genus and species of fruit bat known were taken within the study area in 1975 (see species accounts). Their only known roost was Luplupwintem, a huge doline south-west of Tifalmin. This roost has been deserted for several years. It is imperative that swift action be taken to try to locate any further roosts of this unusual species. We suggest that suitable caves may exist in the Inim Range, between Telefomin and Bolivip in Western Province. This region is topographically similar to the Luplupwintem area, and contains many large dolines. If such roosts are found, the strictest measures must be implemented to protect them from the overexploitation that destroyed the Luplupwintem colony. We suggest that a total ban on

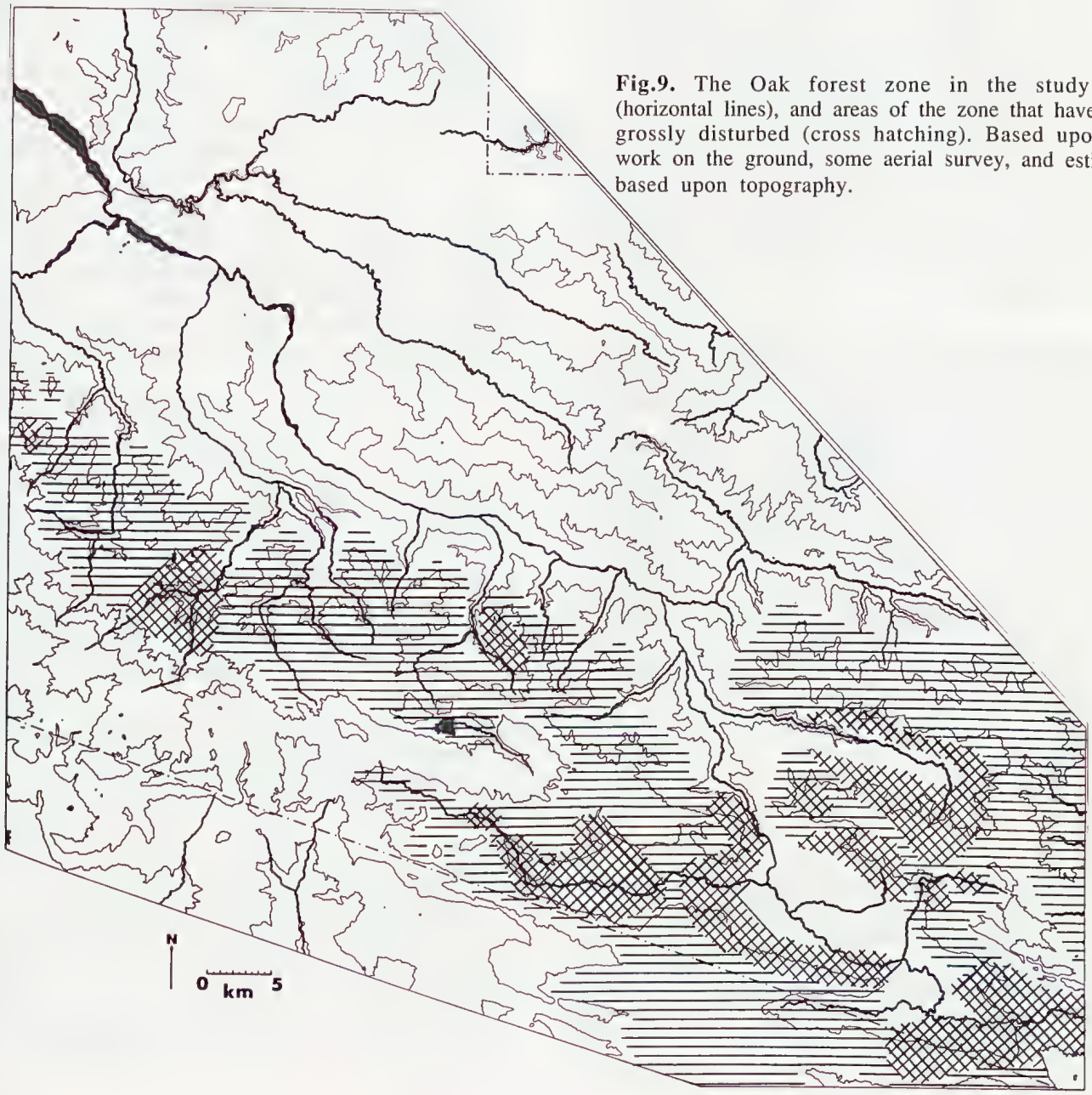


**Fig.9.** The Oak forest zone in the study area (horizontal lines), and areas of the zone that have been grossly disturbed (cross hatching). Based upon our work on the ground, some aerial survey, and estimates based upon topography.

entering the cave may be the best method of protection.

*Conservation of the Oak Forest zone.* Conservation of the Oak Forest zone within the study area is a more difficult but no less vital an objective. This zone (between 1,500 and 2,500 m) is the only known habitat of the seven species listed in Table 8 within Papua New Guinea. Furthermore, the bulk of the mammal species to occur within the region inhabit this zone.

The extent of the Oak Forest zone within the study area is shown in Figure 9. This figure is an estimate based upon topography, the author's experience in this field, and the result of aerial reconnaissance. The extent of disturbed habitat shown is based on the same data. It is clear from this figure that the zone is of limited extent, and that disturbance within it is already considerable. This disturbance will almost certainly grow, particularly in areas of high or growing human population density, such as around Telefomin, Tifalmin and Munbil.

It would be desirable to establish wildlife management areas in parts of this zone, so as to ensure partial, long term protection for large areas of this rich biota. Two areas that may be particularly suitable for such management areas are the Nong River Valley south of Telefomin, and parts of the upper Ilam Valley. The Nong River Valley is particularly important, for it is the only large expanse of undisturbed Oak Forest in the 1,500 to 2,000 m zone in the Telefomin area. It seems to have survived because historically it was at the boundary of two disputing groups, and because it is somewhat difficult of access. There are very few gardens in the area at present, so swift action may allow implementation of a wildlife management area.

**Management of large game species.** The large game species which seem sensitive to overhunting in the area include *Zaglossus bruijnii*, *Dendrolagus dorianus* and *D. goodfellowi*. Traditionally, these species received considerable protection, at least in areas controlled by Telefol. *Zaglossus bruijnii* received almost total protection, while *D. dorianus* could be eaten only by a few senior men. While these restrictions still hold among the more traditionally minded, hunting by others has had a drastic affect on the populations of these species. Perhaps as a remedy, respect for traditional beliefs and their conservation value could be taught in schools in the area. This, plus the remoteness of some of the habitat of these species, may confer long term protection.

## Summary

1) A survey of southern West Sepik Province has shown that between 93 and 120 mammal species inhabit the region. This is the highest diversity recorded for a similar sized region in Australasia.

2) Within this region, maximum diversity is in the midmontane oak forest, where seven species exist that are not found elsewhere in Papua New Guinea.

3) Human activity threatens some mammal species in the region. Further research, and legislative and educational action is urgently needed to avoid extinctions.

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## APPENDIX

Table 1. Times of field work and participants from 1984-1987 for mammal survey of West Sepik Province.

| Year/Month | Locations/working days | Participants |
|---|---|---|
| 1984 (Jan. Feb.) | Yapsiei (12) | Flannery, Van Dyck, Krogh, Gardner, Attenborough |
| | Betavip (16) | Flannery, Van Dyck, Krogh, Gardner, Attenborough |
| | Mount Bubiari (4) | Flannery |
| | Ofektaman (5) | Van Dyck |
| | Sol River (6) | Flannery |
| 1984 (Aug.) | Tifalmin (3) | Seri, Kinbag |
| 1985 (July) | Nong River (6) | Flannery, Steer |
| | Telefomin (2) | Flannery, Steer |
| | Miptigin (4) | Flannery, Steer |
| 1986 (Mar.-May) | Sol River (8) | Flannery, 5 Australian Museum Society volunteers |
| | Munbil (6) | Flannery, 5 Australian Museum Society volunteers |
| | Yapsiei (7) | Flannery, Seri |
| | Betavip (7) | Flannery, Seri |
| | Thurnwald Range (5) | Seri |
| | Telefomin (8) | Flannery, Seri |
| | Yominbip (13) | Flannery, Seri |
| 1987 (Apr.) | Dokfuma (8) | Flannery, Seri, Cogger |
| | Tifalmin (7) | Flannery, Seri, Cogger |
| 1990 (Mar.) | Tifalmin (4) | Flannery |

Table 2. The altitudinal range (Alt.Ra.), habitat preference (Habitat), vertical strata (Vert.St.), body weight (Wt) and diet c the mammal species collected during out survey.

| Taxon | Alt.Ra. | Habitat | Vert.St. | Wt (kgs) | Diet |
|---|---|---|---|---|---|
| *Zaglossus bruijnii* | 0-4,150 | primary forest, alpine grasslands | terrestrial | 7.0-16.0 | worms |
| *Dasyurus albopunctatus* | 0-3,500 | all forest | all | 0.58-0.71 | vertebrates |
| *Antechinus melanurus* | 0-2,800 | all forest | all | 0.026-0.07 | vertebrates/ invertebrates |
| *Antechinus naso* | 1,000-2,800 | primary forest | all | 0.037-0.062 | invertebrates |
| *Microperoryctes longicauda* | 1,000-4,000 | primary forest, alpine grasslands | terrestrial | 0.35-0.67 | invertebrates |
| *Peroryctes raffrayana* | 60-3,900 | primary forest | terrestrial | 0.65-1.0 | invertebrates |
| *Echymipera clara* | 300-1,200 | primary forest | terrestrial | 0.83-1.7 | fruit/invertebrates |
| *Echymipera kalubu* | 0-2,000 | all habitats | terrestrial | 0.45-1.5 | fruit/invertebrates |
| *Echymipera rufescens* | 0-1,200 | secondary forest, grasslands | terrestrial | 1.0-2.0 | fruit/invertebrates |
| *Dendrolagus dorianus* | 800-3,996 | primary forests | all | 6.5-14.5 | leaves |
| *Dendrolagus goodfellowi* | 1,200-2,865 | primary forests | arboreal | 6.7-8.6 | leaves/fruit |
| *Dorcopsis hageni* | 0-400 | primary forests | terrestrial | 5.0-6.0 | leaves/fruit |
| *Dorcopsulus vanheurni* | 800-3,100 | primary forests | terrestrial | 1.5-2.3 | leaves/fruit |
| *Thylogale bruinii* | 0-4,200 | primary forest, alpine grasslands | terrestrial | 3.0-10.0 | leaves/grass |
| *Spilocuscus maculatus* | 0-1,200 | all forest | arboreal | 2.3-6.0 | leaves/fruit |
| *Spilocuscus rufoniger* | 0-1,200 | primary forest | arboreal | 5.5-6.6 | leaves/fruit |
| *Strigocuscus gymnotis* | 0-2,700 | all forest | all | 1.5-4.9 | leaves/fruit |
| *Phalanger orientalis* | 0-1,500 | all forest | arboreal | 1.6-3.5 | leaves/fruit |
| *Phalanger matanim* | 1,500-2,600 | primary forest | arboreal | 1.1-2.0 | leaves/fruit |
| *Phalanger vestitus* | 1,200-2,200 | primary forest | arboreal | 1.4-2.4 | leaves/fruit |
| *Phalanger carmelitae* | 1,400-3,660 | primary forest | arboreal | 1.0-2.0 | leaves/fruit |
| *Phalanger sericeus* | 1,300-3,900 | primary forest | arboreal | 1.7-2.4 | leaves/fruit |
| *Pseudocheirus mayeri* | 1,500-3,600 | primary forest | arboreal | 0.11-0.21 | leaves |
| *Pseudocheirus forbesi* | 500-2,300 | all forest | arboreal | 0.45-0.84 | leaves |

Table 2 (cont'd).

| Taxon | Alt.Ra. | Habitat | Vert.St. | Wt (kgs) | Diet |
|---|---|---|---|---|---|
| *Pseudocheirus corinnae* | 1,200-2,500 | primary forest | arboreal | 0.93-1.1 | leaves |
| *Pseudocheirus cupreus* | 1,200-3,996 | primary forest | arboreal | 1.3-2.3 | leaves |
| *Distoechurus pennatus* | 0-1,900 | secondary forest | arboreal | 0.038-0.062 | fruit/invertebrates |
| *Cercartetus caudatus* | 1,500-3,450 | all forest, grasslands | arboreal | 0.017-0.024 | fruit/invertebrates |
| *Petaurus breviceps* | 0-3,000 | all forest | arboreal | 0.069-0.114 | sap/invertebrates |
| *Dactylopsila trivirgata* | 0-2,300 | all forest | arboreal | 0.23-0.47 | invertebrates |
| *Dactylopsila megalura* | ± 1,400 | primary forest | arboreal | 0.40 | invertebrates |
| *Dactylopsila palpator* | 1,200-2,800 | primary forest | arboreal | 0.32-0.55 | invertebrates |
| *Hydromys chrysogaster* | 0-1,900 | aquatic | terrestrial | 0.21-0.50 | invertebrates |
| *Paraleptomys wilhelmina* | 1,800-2,800 | primary forest | terrestrial | 0.034 | invertebrates |
| *Pogonomys macrourus* | 0-1,800 | all forest | arboreal | 0.03-0.06 | leaves/fruit |
| *Pogonomys championi* | 1,400-2,300 | all forest | arboreal | 0.3-0.06 | leaves/fruit |
| *Mallomys rothschildi* | 1,550-2,500 | primary forest | arboreal | 0.93-1.5 | leaves |
| *Mallomys aroaensis* | 1,000-2,400 | primary forest | arboreal | 0.9-1.5 | leaves |
| *Hyomys goliath* | 1,500-2,800 | all forest | terrestrial | 0.75-0.95 | plant matter |
| *Anisomys imitator* | 0-3,500 | all forest | arboreal | 0.38-0.58 | nuts |
| *Uromys caudimaculatus* | 0-1,925 | all forest | arboreal | 0.40-0.701 | fruit/nuts |
| *Uromys anak* | 850-2,800 | primary forest | arboreal | 0.45-1.0 | fruit/nuts |
| *Lorentzimys nouhuysi* | 80-2,700 | primary forest | arboreal | 0.01-0.02 | ? |
| *Xenuromys barbatus* | 75-1,200 | rocks, primary forest | terrestrial | 0.9-1.1 | fruit |
| *Pogonomelomys ruemmleri* | 1,900-3,600 | primary forest, alpine grasslands | all | 0.03-0.04 | ? invertebrates/fruit |
| *Pogonomelomys sevia* | 1,400-3,100 | all forest, grasslands | all | 0.05 | ? invertebrates/fruit |
| *Pogonomelomys mayeri* | 400-1,300 | all forest | arboreal | 0.08-0.11 | ? invertebrates/fruit |
| *Melomys lanosus* | 1,300-2,800 | primary forest | terrestrial | 0.12 | ? invertebrates/fruit |
| *Melomys rattoides* | 900-1,400 | primary forest | terrestrial | 0.17-0.23 | ? invertebrates/fruit |
| *Melomys rubex* | 900-3,000 | all forest | terrestrial | 0.03-0.06 | ? invertebrates/fruit |
| *Melomys* sp. | 3,200 | alpine, grasslands | terrestrial | 0.04-0.06 | ? invertebrates/fruit |
| *Melomys rufescens* | | secondary forest, grasslands | arboreal | 0.03-0.1 | ? invertebrates/fruit |
| *Melomys platyops* | 0-1,200 | all forest | terrestrial | 0.07-0.10 | ? invertebrates/fruit |
| *Rattus niobe* | 762-4,030 | forest, grasslands | terrestrial | 0.04-0.06 | ? invertebrates/fruit |
| *Rattus* sp. | 1,000-1,400 | forest | terrestrial | 0.06-0.07 | ? invertebrates/fruit |
| *Rattus verecundus* | 150-2,750 | forest | terrestrial | 0.09-0.13 | ? invertebrates/fruit |
| *Rattus steini* | 20-2,800 | forest, grasslands | terrestrial | 0.11-0.22 | ? invertebrates/fruit |
| *Rattus praetor* | 0-1,200 | forest, grasslands | terrestrial | 0.17-0.23 | ? invertebrates/fruit |
| *Rousettus amplexicaudatus* | 0-1,805 | forest | flying | 0.078-0.11 | fruit |
| *Pteropus neohibernicus* | 0-1,000 | forest | flying | 0.73-1.4 | fruit |
| *Dobsonia moluccensis* | 0-2,700 | forest | flying | 0.36-0.60 | fruit |
| *Dobsonia minor* | 0-600 | forest | flying | 0.07-0.09 | fruit |
| *Nytimene cyclotis* | 830-2,300 | forest | flying | 0.05 | fruit |
| *Nytimene albiventer* | 0-1,650 | forest | flying | 0.02-0.03 | fruit |
| *Nytimene aello* | 0-990 | forest | flying | 0.08-0.09 | fruit |
| *Paranyctimene raptor* | 0-1,000 | forest | flying | 0.02-0.03 | fruit |
| *Macroglossus minimus* | 0-1,000 | forest | flying | 0.01-0.02 | nectar |
| *Syconycteris hobbit* | 2,300-2,400 | forest | flying | – | nectar |
| *Syconycteris australis* | 0-3,000 | forest | flying | 0.01-0.02 | nectar |
| *Nyctophilus microtis* | 200-990 | forest | flying | 0.006-0.008 | insects |
| *Pipistrellis collinus* | 1,700-2,450 | forest | flying | 0.007 | insects |
| *Kerivoula muscina* | 20-1,800 | forest | flying | 0.005 | insects |
| *Miniopterus australis* | 0-1,500 | forest | flying | 0.007-0.009 | insects |
| *Miniopterus* sp. | 3,200 | grassland | flying | 0.01 | insects |
| *Miniopterus macroneme* | 0-2,300 | forest | flying | 0.008-0.01 | insects |
| *Miniopterus medius* | + 1,360 | forest | flying | 0.01 | insects |
| *Miniopterus magnater* | 0-2,100 | forest | flying | 0.01 | insects |
| *Hipposideros ater* | | forest | flying | 0.01 | insects |
| *Hipposideros corynophyllus* | 1,600-1,800 | forest | flying | 0.015 | insects |
| *Hipposideros wollastoni* | 550-2,000 | forest | flying | 0.005-0.008 | insects |
| *Hipposideros cervinus* | | forest | flying | 0.003-0.01 | insects |
| *Hipposideros diadema* | | forest | flying | 0.03-0.04 | insects |
| *Rhinolophus arcuatus* | | forest | flying | | insects |
| *Emballonura beccarii* | 0-1,300 | forest | flying | 0.004-0.005 | insects |
| *Emballonura raffrayana* | 0-1,320 | forest | flying | 0.004-0.005 | insects |
| *Emballonura nigrescens* | 0-1,000 | forest | flying | 0.003-0.004 | insects |

Table 3. Telefol and Mianmin names for mammal taxa collected during this work.

| Taxon | Telefol | Mianmin |
|---|---|---|
| *Zaglossus bruijnii* | Egil | Yakeil |
| *Dasyurus albopunctatus* | Kutinim | Tangtangib |
| *Antechinus melanurus* | Foomkayok | Bumtaing |
| *Antechinus naso* | — | — |
| *Microperoryctes longicaudata* | Warem | — |
| *Peroryctes raffrayana* | Ibin | Duwin |
| *Echymipera clara* | — | Kiyok |
| *Echymipera rufescens* | — | Aiyal |
| *Echymipera kalubu* | Aiyal | Aiyal |
| *Distoechurus pennatus* | — | Mayfagam |
| *Cercartetus caudatus* | Finareng | — |
| *Petaurus breviceps* | Silek | Mayfagam |
| *Dactylopsila trivirgata* | Triok | Kwidiaim |
| *Dactylopsila megalura* | Defem, Triok | — |
| *Dactylopsila palpator* | Triok | — |
| *Dorcopsulus vanheurni* | Autom | Soyabu |
| *Dorcopsis hageni* | — | Titiabu |
| *Thylogale brunii* | Simulim | Sumul |
| *Dendrolagus dorianus* | D'bol | — |
| *Dendrolagus goodfellowi* | Timboyok | Yemma, Timboyok |
| *Pseudocheirus forbesi* | Sobim | — |
| *Pseudocheirus mayeri* | Dom | — |
| *Pseudocheirus corrinae* | Dabam | — |
| *Pseudocheirus cupreus* | Kayang | Hito |
| *Strigocuscus gymnotis* | Quoyam | Quoyam |
| *Phalanger orientalis* | Ibim | Maetol, Ibim, Aligin |
| *Phalanger vestitus* | Nelem | — |
| *Phalanger carmelitae* | Tim Matanim | — |
| *Phalanger matanim* | Matanim | — |
| *Phalanger sericeus* | Kutip | Satol |
| *Phalanger maculatus* | Selip | Tekeib |
| *Phalanger rufoniger* | Selip | Tekeib |
| *Hydromys chrysogaster* | ? Bidok | Ayam |
| *Pogonomys macrourus* | Elam | Ilam |
| *Pogonomys championi* | Elam | — |
| *Mallomys rothschildi* | Resen | — |
| *Mallomys aroaensis* | — | — |
| *Hyomys goliath* | Trossin | ? Afut |
| *Anisomys imitator* | Apsal | — |
| *Uromys anak* | Quotal | — |
| *Uromys caudimaculatus* | Ditip | Quaterib |
| *Xenuromys barbatus* | — | Boboyomin |
| *Lorentzimys nouhuysi* | Ifum | — |
| *Pogonomelomys ruemmleri* | Karung | — |
| *Pogonomelomys mayeri* | Karung | — |
| *Pogonomelomys sevia* | Karung | — |
| *Melomys lanosus* | Mankan | — |
| *Melomys rattoides* | — | Temeya |
| *Melomys rubex* | Ingat | Briazu |
| *Melomys rufescens* | Aubil | Dawan |
| *Melomys moncktoni* | — | Abul |
| *Rattus niobe* | Titok | — |
| *Rattus verecundus* | ? Titok | — |
| *Rattus steini* | Senok | Senok |
| *Rattus praetor* | — | Senok |
| *Nyctophilus microtis* | — | — |
| *Pipistrellus collinus* | — | — |
| *Emballonura beccarii* | — | — |
| *Emballonura raffrayana* | — | — |
| *Emballonura nigrescens* | — | Heba-heba |
| *Miniopterus australis* | Ibrup | — |
| *Miniopterus magnater* | Ibrup | — |
| *Miniopterus macrocneme* | Ibrup | — |

Table 3 (cont'd).

| Taxon | Telefol | Mianmin |
|---|---|---|
| *Hipposideros corynophyllus* | — | — |
| *Hipposideros wollastoni* | — | — |
| *Hipposideros cervinus* | — | — |
| *Hipposideros diadema* | — | — |
| *Rousettus amplexicaudatus* | — | Sagamal |
| *Pteropus neohibernicus* | — | Sewi |
| *Macroglossus minimus* | — | Raulabo |
| *Syconycteris australis* | Timinim | Raulabo |
| *Syconycteris hobbit* | Timinim | — |
| *Dobsonia moluccensis* | Segam | Ketab |
| *Dobsonia minor* | — | — |
| *Nyctimene cyclotis* | ? Brulim | — |
| *Nyctimene albiventer* | — | Raulabo |
| *Nyctimene aello* | — | ? Uleulelabu |
| *Paranyctimene raptor* | — | ? Uleulelabu, Raulabo |

Table 4. Rainfall data (in mm) for some localities within the study area. The data for Yapsiei is approximate as some figures are underestimates and others are missing (R. Attenborough, personal communication).

| | Jan. | Feb. | Mar. | Apr. | May | June | July | Aug. | Sept. | Oct. | Nov. | Dec. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tifalmin 1980 | 23 | 182 | 370 | 187 | 160 | | | | | | | |
| Yapsiei 1980 | 448 | 265 | 175 | 802 | 750 | 205 | 433 | | 544 | 457 | 444 | 470 |
| Yapsiei 1982 | 260 | 592 | 450 | 887 | 481 | 630 | 259 | 383 | 228 | 383 | 407 | 480 |
| Telefomin 1980 | 192 | 164 | 365 | 320 | 348 | 264 | 197 | | | 266 | 188 | 266 |
| Telefomin 1982 | | 173 | 132 | 319 | 227 | 246 | 80 | | 41 | 161 | 130 | 97 |
| Telefomin 1983 | 147 | 260 | 175 | 147 | 327 | 222 | 84 | 57 | 283 | 283 | 245 | 249 |
| Telefomin 1984 | 347 | 319 | 294 | 394 | 520 | 422 | 423 | 385 | 447 | 382 | 168 | 300 |
| Telefomin 1985 | 296 | 389 | 193 | 325 | 211 | 224 | 260 | 444 | 334 | 343 | 205 | 280 |

Table 5. Cranial measurements of *Dendrolagus dorianus* specimens held in the Australian Museum used in this study. CBL = condylobasal length, BIZYW = bizygomatic width, MASTOID W = mastoid width, NAS.L. = nasal length, X = mean, R = range, N = sample size, L = length, W = width, M2/-M2/W = width from the external faces of the molars.

| | | *D.d. stellarum* n.sp. | | *D.d. notatus* | | *D.d. dorianus* | |
|---|---|---|---|---|---|---|---|
| | | male | female | male | female | male | female |
| CBL | X | 118.1 | 110.8 | 118.3 | 115.5 | 125.5 | 121.0 |
| | R | 117.5-118.7 | 110.8 | 112.8-122.8 | 111.0-119.6 | 123.1-128.5 | 121.0 |
| | N | 2 | 1 | 3 | 7 | 4 | 1 |
| BIZYW | X | 64.8 | 66.2 | 67.1 | 66.5 | 74.1 | 71.9 |
| | R | 61.0-68.6 | 66.2 | 66.2-71.5 | 61.4-70.3 | 71.3-76.7 | 71.9 |
| | N | 2 | 1 | 3 | 7 | 4 | 1 |
| MASTOID W | X | 46.8 | 42.1 | 50.3 | 50.3 | 52.4 | 48.0 |
| | R | 42.7-50.9 | 42.1 | 49.2-52.2 | 47.9-53.3 | 47.5-57.1 | 48.0 |
| | N | 2 | 1 | 3 | 7 | 4 | 1 |
| NAS.L. | X | 41.4 | 42.0 | 44.3 | 41.6 | 52.1 | 47.1 |
| | R | 40.5-42.3 | 42.0 | 42.2-45.7 | 40.1-42.8 | 49.0-56.3 | 47.1 |
| | N | 2 | 1 | 3 | 6 | 4 | 1 |
| P3-M5/L | X | 35.7 | 33.5 | 37.5 | 36.8 | 38.1 | 38.6 |
| | R | 35.1-36.2 | 33.5 | 36.5-38.5 | 35.4-39.5 | 36.5-39.1 | 38.6 |
| | N | 2 | 1 | 3 | 7 | 5 | 1 |
| P3/L | X | 9.8 | 9.2 | 10.7 | 10.6 | 10.8 | 10.9 |
| | R | 9.7-9.9 | 9.2 | 10.4-11.1 | 10.0-11.2 | 10.2-11.5 | 10.9 |
| | N | 2 | 1 | 3 | 7 | 5 | 1 |
| P3/W | X | 6.3 | 5.8 | 6.4 | 6.2 | 6.6 | 6.4 |
| | R | 6.2-6.3 | 5.8 | 6.0-6.7 | 5.5-6.8 | 6.2-7.0 | 6.4 |
| | N | 2 | 1 | 3 | 7 | 5 | 1 |
| N2/W | X | 5.9 | 5.7 | 6.4 | 6.2 | 6.3 | 6.1 |
| | R | 5.8-5.9 | 5.7 | 6.0-6.6 | 5.9-6.6 | 6.1-6.5 | 6.1 |
| | N | 2 | 1 | 3 | 7 | 4 | 1 |
| M2/-M2/W | X | 32.2 | 30.0 | 32.9 | 32.6 | 34.1 | 31.5 |
| | R | 31.9-32.4 | 30.0 | 31.5-34.7 | 31.5-34.0 | 32.9-35.1 | 31.5 |
| | N | 2 | 1 | 3 | 7 | 4 | 1 |

Table 6. External measurements of *Miniopterus* specimens (see text). X = mean, R = range, N = sample size, STD = standard deviation.

| | | *Miniopterus magnater* | *Miniopterus australis* | *Miniopterus macrocneme* | *Miniopterus* sp. | *Miniopterus medius* |
|---|---|---|---|---|---|---|
| Forearm | X | 49.3 | 42.3 | 42.1 | 46.4 | 47.1 |
| | R | 45.0-51.3 | 41.0-45.0 | 40.0-43.5 | | |
| | N | 10 | 12 | 14 | 1 | 1 |
| | STD | 2.22 | 1.05 | 1.07 | | |
| Head-body | X | 51.1 | 41.8 | 46.0 | 47.3 | 59.5 |
| | R | 44.3-55.8 | 38.0-47.0 | 42.0-50.0 | | |
| | N | 8 | 10 | 19 | 1 | 1 |
| | STD | 4.18 | 2.81 | 2.17 | | |
| Tibia | X | 20.1 | 12.0 | 18.5 | 19.3 | 20.0 |
| | R | 18.9-20.8 | 11.0-13.0 | 17.5-19.4 | | |
| | N | 10 | 12 | 19 | 1 | 1 |
| | STD | 0.65 | 0.45 | 0.57 | | |
| Ear | X | 11.5 | 10.1 | 9.7 | 11.2 | 14.7 |
| | R | 9.0-13.5 | 8.0-12.0 | 8.6-11.0 | | |
| | N | 9 | 12 | 19 | 1 | 1 |
| | STD | 1.31 | 1.10 | 0.75 | | |
| Weight | X | 15.1 | 7.9 | 8.6 | 10.5 | 12.1 |
| | R | 11.0-18.0 | 7.0-9.0 | 7.2-10.0 | | |
| | N | 10 | 12 | 33 | 1 | 1 |
| | STD | 2.26 | 0.56 | 0.78 | | |

Table 7. Comparisons of mammals collected during our work (A) and that of the 3rd Archbold Expedition (B). The latter is from the literature only; Alt.Ra. = Altitudinal range.

| Taxon | A | | B | |
|---|---|---|---|---|
| | No. | Alt.Ra. | No. | Alt.Ra. |
| *Zaglossus bruijnii* | 2 | 1,300-1,500 m ? | 1 | 2,800 m |
| *Murexia longicaudata* | – | | 10 | 75 m |
| *Myoictis melas* | – | | 13 | upper Idenburg Valley |
| *Phascolosorex doriae* | – | | ? | 1,200-1,800 m |
| *Neophascogale lorentzii* | – | | 96 | 2,400-3,500 m |
| *Antechinus naso* | 1 | 1,400 m | 22 | 1,500-2,400 m |
| *Antechinus wilhelmina* | – | | 11 | 2,100-2,800 m |
| *Antechinus melanurus* | 6 | 240-2,300 m | 4 | 50-450 m |
| *Dasyurus albopunctatus* | 3 | 1,000-2,300 m | 17 | Idenburg River |
| *Peroryctes raffrayana* | 6 | 600-1,400 m | 31 | 75-2,150 m |
| *Microperoryctes longicauda* | 4 | 1,400-2,400 m | 74 | 1,200-3,950 m |
| *Echymipera clara* | 7 | 200-400 m | 13 | 75-850 m |
| *Echymipera kalubu* | 20 | 120-1,400 m | 36 | 50-75 m |
| *Echymipera rufescens* | 1 | 200 m | 3 | 75 m |
| *Cercartetus caudatus* | 22 | 1,400-3,200 m | 30 | 1,500-4,000 m |
| *Distoechurus pennatus* | 3 | 160-1,000 m | – | |
| *Petaurus breviceps* | 17 | 200-2,300 m | – | |
| *Dactylopsila trivirgata* | 2 | 1,300 m | – | |
| *Dactylopsila palpator* | 7 | 1,500-1,800 m | 9 | 850-2,800 m |
| *Dactylopsila megalura* | 4 | about 1,400 m | – | |
| *Pseudocheirus mayeri* | 13 | 1,500-3,200 m | 40 | "Mount Wilhelmina" |
| *Pseudocheirus canescens* | – | | 2 | 100 m |
| *Pseudocheirus forbesi* | 40 | 1,400-2,400 m | – | |
| *Pseudocheirus corinnae* | 10 | 1,500-2,300 m | 21 | 2,100-2,450 m |
| *Pseudocheirus cupreus* | 20 | 1,800-2,800 m | 14 | 1,650-1,900 m |
| *Spilocuscus rufoniger* | 4 | 120-1,200 m | 1 | 75 m |
| *Spilocuscus maculatus* | 1 | about 600 m | 24 | 50 m Idenburg River |
| *Phalanger orientalis* | 31 | 120-1,500 m | 5 | Middle Idenburg River |
| *Phalanger sericeus* | 13 | 1,500-2,600 m | 22 | 3,000-3,300 m |
| *Phalanger matanim* | 4 | 1,500-2,600 m | – | |
| *Phalanger vestitus* | 13 | 1,400-1,600 m | – | |
| *Phalanger carmelitae* | 7 | 1,500-2,400 m | – | |
| *Strigocuscus gymnotis* | 37 | 200-2,600 m | 10 | 75 m |
| *Dorcopsulus vanheurni* | 6 | 1,400-1,800 m | 19 | 1,200-2,700 m |
| *Dorcopsis hageni* | 9 | 120-200 m | ? | Middle Idenburg River |
| *Thylogale brunii* | 1 | 600 m | – | |
| *Dendrolagus dorianus* | 4 | 2,800-3,200 m | – | |
| *Dendrolagus goodfellowi* | 4 | 1,000-1,300 m | – | |
| *Paraleptomys wilhelmina* | 1 | 1.800 m | 78 | 1,800-2,800 m |
| *Pseudohydromys occidentalis* | – | | 5 | 3,225-3,600 m |
| *Microhydromys richardsoni* | – | | 1 | 850 m |
| *Hydromys habbema* | – | | 29 | 3,225-3,600 m |
| *Hydromys chrysogaster* | 3 | 200-900 m | 7 | 800 m |
| *Parahydromys asper* | – | | 16 | 1,200-2,800 m |
| *Lorentzimys nouhuysi* | 11 | 1,400-2,600 m | 12 | 850-2,700 m |
| *Macruromys major* | – | | 4 | 1,200 m |
| *Mallomys rothschildi* | 6 | 1,500-2,300 m | 14 | 2,200-3,800 m |
| *Mallomys aroaensis* | 1 | 1,600 m | – | |
| *Hyomys goliath* | 3 | 1,400-1,800 m | 5 | 2,200-2,800 m |
| *Anisomys imitator* | 2 | 1,400-2,300 m | 84 | 1,200-2,800 m |
| *Pogonomys championi* | 41 | 1,400-2,300 m | – | |
| *Pogonomys sylvestris* | – | | 66 | 2,200-2,800 m |
| *Pogonomys macrourus* | 30 | 900-1,500 m | 1 | 850 m |
| *Xenuromys barbatus* | 3 | 400-1,200 m | 1 | 75 m |
| *Uromys caudimaculatus* | 3 | 400-1,500 m | 20 | 50-1,200 m |
| *Uromys anak* | 3 | 1,500-1,800 m | 15 | 850-2,800 m |
| *Pogonomelomys mayeri* | 2 | 1,320-1,400 m | 1 | 400 m |
| *Pogonomelomys ruemmleri* | 2 | 2,800-3,200 m | 43 | 2,800-3,500 m |
| *Pogonomelomys sevia* | 1 | 1,400 m | – | |
| *Melomys lanosus* | 16 | 1,800-2,300 m | 119 | 1,500-2,800 m |
| *Melomys rattoides* | 17 | 900-1,100 m | 31 | 850-1,200 m |

Table 7 (cont'd).

| Taxon | A | | B | |
|---|---|---|---|---|
| | No. | Alt.Ra. | No. | Alt.Ra. |
| *Melomys lutillus* | – | | 151 | 1,600-2,200 m |
| *Melomys rufescens* | 25 | 200-1,500 m | 6 | 1,600-2,200 m |
| *Melomys rubex* | 33 | 1,400-3,200 m | | ? |
| *Melomys platyops* | 10 | 160-240 m | | ? |
| *Rattus praetor* | 29 | 200-900 m | 8 | 75-1,500 m |
| *Rattus steini* | 95 | 160-2,300 m | 148 | 1,600-2,800 m |
| *Rattus verecundus* | 1 | 2,600 m | – | |
| *Rattus richardsoni* | – | | 56 | 3,560-4,050 m |
| *Rattus* sp. cf. *R. niobe* ? | 3 | 1,000-1,400 m | – | ? |
| *Rattus niobe arrogans* | 19 | 3,200 m | ±500 | 2,200-4,000 m |
| *Rattus niobe pococki* | 6 | 1,400-2,300 m | 67 | 1,800-2,150 m |
| *Melomys albidens* | – | | 3 | 3,225 m |
| *Pteropus neohibernicus* | 5 | 160-240 m | ? | Idenburg River area |
| *Pteropus macrotis* | – | | 7 | Idenburg River area |
| *Dobsonia moluccensis* | 15 | 160-1,500 m | 6 | Idenburg River area |
| *Dobsonia minor* | 10 | 200-240 m | 7 | Idenburg River area |
| *Nyctimene albiventer* | 39 | 200-1,000 m | 1 | Idenburg River area |
| *Nyctimene cyclotis* | 1 | 2,300 m | – | |
| *Nyctimene aello* | 4 | 200 m | – | |
| *Paranyctimene raptor* | 10 | 200-900 m | – | |
| *Rousettus amplexicaudatus* | 27 | 200 m | – | |
| *Macroglossus minimus* | 29 | 200-1,000 m | – | |
| *Syconycteris hobbit* | 1 | 2,300 m | – | |
| *Syconycteris australis* | 132 | 200-2,300 m | 3 | Idenburg River |
| *Hipposideros calcaratus* | – | | 10 | Idenburg River |
| *Hipposideros cervinus* | 4 | 200-1,300 m | – | |
| *Hipposideros ater* | 1 | 1,600 m | – | |
| *Hipposideros diadema* | 1 | 200 m | – | |
| *Hipposideros corynophyllus* | 25 | 1,500-1,800 m | – | |
| *Hipposideros wollastoni* | 31 | 1,400-1,800 m | – | |
| *Rhinolophus arcuatus* | 5 | 1,600 m | – | |
| *Miniopterus magnater* | 11 | 1,500-2,100 m | 2 | Upper Idenburg River |
| *Miniopterus medius* | 1 | 1,340 m | – | |
| *Miniopterus* sp. | 1 | 3,200 m | – | |
| *Miniopterus macrocneme* | 38 | 1,500-3,200 m | – | |
| *Miniopterus australis* | 12 | 1,500 m | – | |
| *Nyctophilus bifax* | – | | 1 | 850 m |
| *Nyctophilus microtis* | 1 | 200 m | – | |
| *Pipistrellus collinus* | 1 | 2,300 m | – | |
| *Kerivoula muscina* | 3 | 1,600 m | – | |
| *Emballonura beccarii* | 30 | 1,300 m | – | |
| *Emballonura raffrayana* | 26 | 900-1,300 m | – | |
| *Emballonura nigrescens* | 13 | 200-1,000 m | – | |

Table 8. Altitudinal range (in metres) of the seven western and endemic species found in the study area. * = based on local informants only; # = from the Tabubil area, where altitudinal zones are markedly depressed.

| Taxon | range in study area | range elsewhere |
|---|---|---|
| *Phalanger matanim* | 1,500-2,600 | — |
| *Hipposideros corynophyllus* | 1,500-2,000 | — |
| *H. wollastoni* | 1,400-1,800 | 580#-1,800 |
| *Dactylopsila megalura* | 1,500-2,000* | 1,400-2,000 |
| *Paraleptomys wilhelmina* | 1,800 | 1,800-2,800 |
| *Pogonomys championi* | 1,400-2,300 | 1,400-2,800 |
| *Melomys lanosus* | 1,800-2,300 | 1,500-2,800 |

# Four New Species of *Micromaldane* (Polychaeta: Maldanidae) from Eastern Australia

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ABSTRACT. Four new species of *Micromaldane* (Polychaeta: Maldanidae) found intertidally on the eastern rocky coast and coral reefs of Australia are described. A key to all species of *Micromaldane* is provided. The generic definition is discussed and emended.

ROUSE, G.W., 1990. Four new species of *Micromaldane* (Polychaeta: Maldanidae) from eastern Australia. Records of the Australian Museum 42(2): 209–219.

The Nicomachinae is one of five subfamilies within the Maldanidae. It is a small group with only three genera: *Nicomache* Malmgren, 1865, *Petaloproctus* Quatrefages, 1865, and *Micromaldane* Mesnil, 1897 (Fauchald, 1977). To date there has been only one previous record of the genus *Micromaldane* from Australian waters, an unidentified species from Heron Island, Great Barrier Reef (Reichelt, 1979).

The type species *Micromaldane ornithochaeta* Mesnil, 1897, originally found on the French Atlantic coast, has subsequently been recorded from Ireland (Southern, 1914), Norfolk (Hammond, 1966), British Colombia (Berkeley & Berkeley, 1962) and the Antarctic (Fauvel, 1951). To date there have been two additional species described: *Micromaldane bispinosa* Hartmann-Schröder, 1962 from the Red Sea and *M. jonesi* Kumaraswamy Achari, 1968, from the Indian Ocean.

While maldanids are regarded as common in continental shelf sediments (Fauchald, 1977) there have been few records of this family in Australian waters (see Day & Hutchings, 1979), possibly due to lack of sampling in these areas. Examination of the intertidal algal mats of the rocky shores around Sydney, New South Wales has revealed two new species of *Micromaldane*. An additional two new species have also been found from One Tree Reef, Great Barrier Reef.

## Materials and Methods

Collections of algal mats were made from the lower intertidal zone at the sites indicated in the text. This material was then sorted under a binocular microscope. All species described here have distinctive sandy tubes and have to be coaxed out by probing the head of the worm so that it

retreats out of the posterior end of the tube. This also results in any larvae in the tubes being expelled. Specimens of all species were examined alive before fixation in 10% sea-water formalin and transfered to 70% ethanol (after washing). For scanning electron microscopy (S.E.M.), specimens were dehydrated in ethanol and critical point dried with $CO^2$ and coated with gold or platinum (200Å) before viewing with a Philips 505 S.E.M. Photomicrographs were taken with a Leitz Dialux photomicroscope using Interference Contrast and an Orthomat camera. Descriptions of new species are based on the alcohol preserved holotype and some S.E.M. observations of paratypes, the variation is based on alcohol preserved paratypes. Line drawings of setae were made from photographs from paratype material.

The following abbreviations have been used: AM – Australian Museum, Sydney; BMNH – British Museum of Natural History, London; HZM – Zoologisches Institut und Zoologisches Museum der Universität, Hamburg; USMN – National Museum of Natural History, Smithsonian Institution, Washington D.C.

## Systematics

### Nicomachinae

Nicomachinae Arwidsson, 1907: 82.—Day, 1967: 617.—Fauchald, 1977: 38.

**Diagnosis.** Nuchal grooves straight or curved. No cephalic plate. Pygidium on a foliaceous plate or sunken in a funnel that is crenulate or rimmed with cirri. Segments without collars. Neuropodial hooks usually in a single row.

### *Micromaldane* Mesnil, emended

*Micromaldane* Mesnil, 1897: 146–148, figs 1–2, pl.6 figs 1–4.—Fauvel, 1927: 193.—Day, 1967: 619.—Kumaraswamy Achari, 1968: 269.—Fauchald, 1977: 40.

**Type species.** *Micromaldane ornithochaeta* Mesnil, 1897, by original designation.

**Diagnosis.** Nicomachinae with strongly curved avicular, rostrate, uncini on all setigers. Notosetae and neurosetae on all setigers. Notopodia short and rounded, neuropodia with elongated tori. Notosetae of 3 kinds: stout, spatulate or straight lancet-type setae with striations, delicate geniculate setae with fine teeth along one margin and/or fine bordered capillary setae. Anal plaque evenly crenated without cirri.

**Comments.** Since the original description of *Micromaldane ornithochaeta* Mesnil, 1897, several authors have expressed doubts as to the validity of this genus and have regarded *M. ornithochaeta* as a juvenile of *Nicomache* which can occur in the same habitat (Fauvel, 1927; Hammond, 1966; Day, 1967). *Nicomache*, however has no uncini on the first setiger and it is also notable that Mesnil (1897) noted greyish ova in his original description of *M. ornithochaeta*. Rouse & Jamieson (1987) described the ultrastructure of the spermatozoa of an unidentified species of *Micromaldane* (as *Micromaldane* sp.) further demonstrating the validity of the genus, although examination of the type species is necessary.

From the observations on the four new species in this study, and by Kumaraswamy Achari (1968) on *M. jonesi*, it is apparent that a maximum number of setigers is reached by each species. This has been used as a specific character (see key to species).

### Key to the Species of *Micromaldane* *

1. Lancet-type notosetae spatulate (Fig.5l) ..... 2
—— Lancet-type notosetae straight ..... 3
2. Maximally 17 setigers ..... *M. ornithochaeta*
—— Maximally 19 setigers ..... *M. jonesi*
3. Preanal asetigerous segment present ..... 4
—— Pre-anal asetigerous segment absent ..... 5
4. Maximally 21 setigers ..... *M. bispinosa*
—— Maximally 25 setigers ..... *M. androgyne*
5. More than 20 setigers ..... 6
—— Maximally 19 setigers ..... *M. nutricula*

6. Maximally 21 setigers ..... *M. rubrospermatheca*

—— Maximally 23 setigers ..... *M. pamelae*

*This key is not meant to imply phylogenetic relationships.

### *Micromaldane androgyne* n.sp.

Figs 1a–i, 5a–b

**Material examined.** HOLOTYPE: Queensland, Great Barrier Reef, One Tree Reef, 23°30'S 152°05'E (AM W 20207). PARATYPES: Queensland, Great Barrier Reef, One Tree Reef, 23°30'S 152°05'E 4 (AM W 20208, in 70% alcohol), 2 (AM W 20209, on S.E.M. stub), 4 (BMNH ZB 1990. 4-7), 4 (HZM P-20208), 4 (USNM). All collected 2 Dec. 1988 by the author.

**Description.** Holotype a complete mature simultaneous hermaphrodite with 25 setigers and 1 preanal asetigerous segment and total length of 5.5 mm. Figure 1a shows a mature adult with 25 setigers.

Head and anterior 5 setigers white, remainder of body transparent before turning white after fixation. Prostomium with slight thickening around dorsal edge (Fig.1c). 2 clusters of eyespots in front of buccal opening. Nuchal grooves straight (Fig.1c).

Notosetae of 2 types: straight, stout, lancet-shaped setae

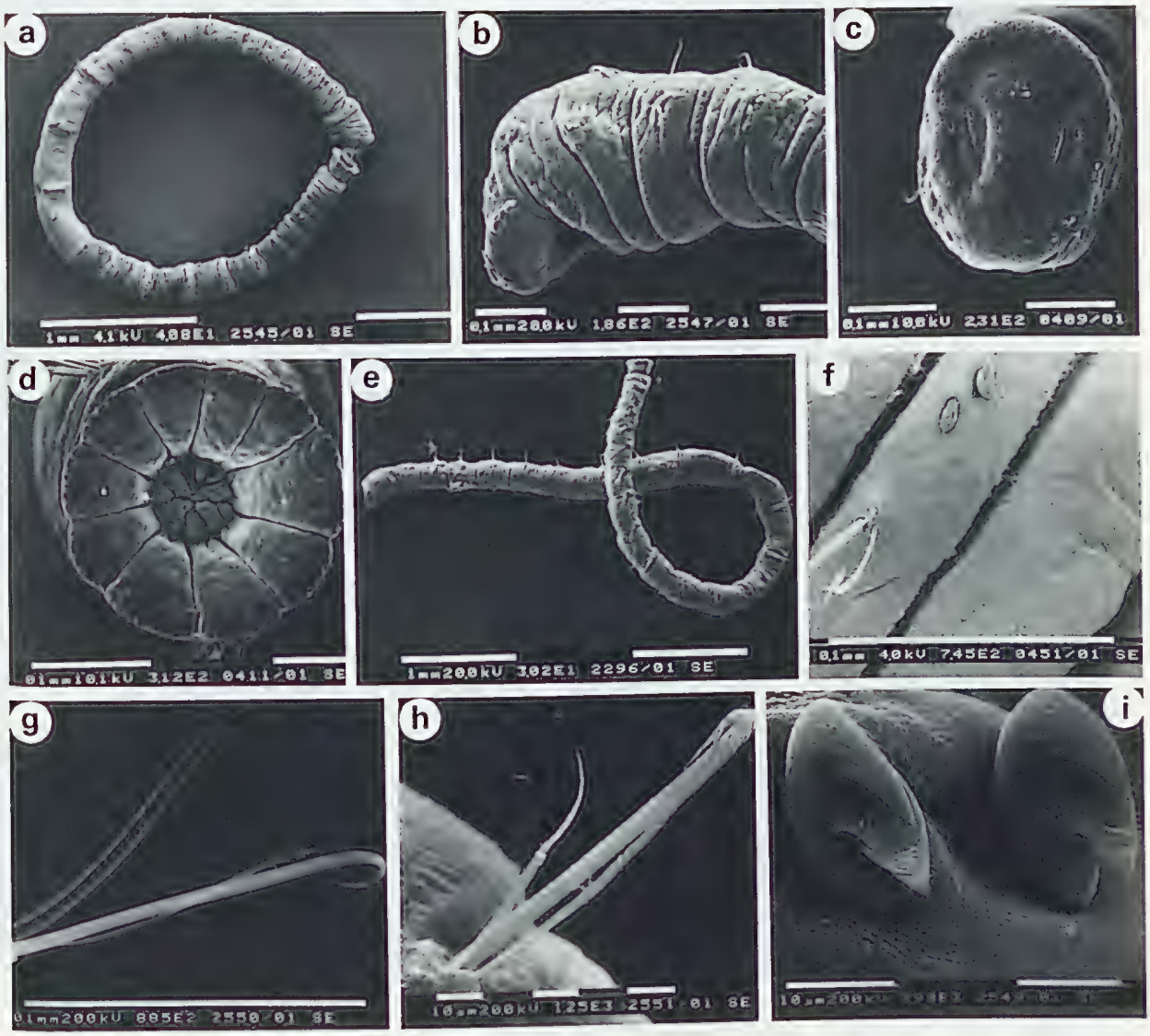


**Fig.1.** *Micromaldane androgyne* n.sp. (AM W 20209): a. S.E.M. side view of whole animal. b. S.E.M. side view of head and anterior setigers. c. S.E.M. frontal view of head showing small nuchal grooves. d. S.E.M. view of anal plaque showing crenations and anus. e. S.E.M. view of whole animal. Note bilateral symmetry of anal plaque with ventral region of the plaque projecting more than the dorsal region. f. S.E.M. of last setiger and preanal asetigerous segment. g. S.E.M. view of notosetae of 7th setiger. h. S.E.M. view of notosetae of 20th setiger. i. S.E.M. view of uncini showing main fang, subrostral barbules, four minor teeth over main fang and small lateral teeth. Scale indicated by white bar and bottom left measurement on each figure.

(Figs 1g,h, 5b) or delicate capillary setae with fine teeth along one margin (Figs 1g,h, 5a). All setigers have 1 or 2 lancet setae and 0–1 capillary setae. Uncini of neuropodia lie in single row on all setigers (Fig.1a). Setigers 1–6 have 2–4 uncini. Setigers 7–14 have 5–9 uncini and setigers 15–25 have 2–4 uncini. All uncini strongly curved with long shafts and prominent main fang surrounded by subrostral barbules. 4 smaller teeth and numerous lateral teeth lie over main fang (Fig.1i).

Setigers 8–11 longer than other setigers (Fig.1a,e). After setiger 11 setigers become progressively shorter until preanal asetigerous segment (Fig.1a,e,f). Anal plaque bears no cirri but is gently crenated (Fig.1d). Anal plaque bilaterally symmetrical and projects more on ventral side than on dorsal side (Fig.1e).

Tube housing holotype, composed of mucous and small particles of calcium carbonate sediment, also contained 2 directly developing larvae at same stage of development and whitish in colour. Body of holotype with a small number of white oocytes in coelomic cavity and several groups of spermatids connected by cytophore. Oogenesis solitary with oocytes floating free in the coelom during vitellogenesis.

**Variation.** The maximum number of setigers appears to be 25. All specimens found, including smaller juvenile specimens, have oocytes and several clumps of developing sperm. No specimens were found with sperm only and due to the paucity of sperm and the absence of spermathecae it is presumed that this species is self-fertilising. All large mature specimens were found to have larvae in their tubes. The number of setae per parapodia of the paratypes is similar to the holotype. Paratype size range from 4 to 5.5 mm in length.

The colour patterning of the anterior region of the body is variable. While most specimens have a white anterior end with the remainder of the body transparent (before preservation) some specimens had no pigmentation of the anterior end.

**Comments.** No other species of *Micromaldane* has been described with specimens having up to a maximum of 25 setigers (see Table 1). Also *M. ornithochaeta* Mesnil, 1897 and *M. jonesi* Kumaraswamy Achari, 1968 have spatulate lancet notosetae (Fig.5l), in contrast to the straight lancet notosetae of *M. androgyne* n.sp. *Micromaldane bispinosa* Hartmann-Schröder, 1960 has straight lancet notosetae and a preanal asetigerous segment however it differs from *M. androgyne* n.sp. in having fewer setigers and two types of uncini. *Micromaldane androgyne*n.sp. is clearly different from the three species described here in the number of setigers, shape of anal plaque and in that it is a simultaneous hermaphrodite.

**Habitat.** Found intertidally, gravid all year round, amongst mats of the red algae *Laurencia* sp. on the upper reef crest on the north-eastern side of One Tree Reef.

**Distribution.** Type locality only.

**Etymology.** Specific name from the latin *androgynus* meaning hermaphrodite.

### *Micromaldane nutricula* n.sp.

Figs 2a–k, 5c–e

**Material examined.** HOLOTYPE: New South Wales, Port Jackson, Bottle and Glass Rocks, 33°58'S 151°00'E, intertidal, (AM W 20210). PARATYPES: New South Wales, Port Jackson, Bottle and Glass Rocks, 33°58'S 151°00'E, intertidal, 4 (AM W 20211, in 70% alcohol), 3 (AM W 20212, on the S.E.M. stub), 4 (BMNH ZB 1990. 8-11), 4 (HZM P-20209), 4 (USNM). All collected 10 Oct. 1988 by the author.

**Description.** Holotype is a complete mature female

Table 1. Characteristics of *Micromaldane*

| Species of *Micromaldane* | Type locality | Setigers | Pre-anal aset. seg. | Notosetae (lancet type) | Length (mm) |
|---|---|---|---|---|---|
| *M. androgyne* n.sp. Rouse, 1990 | Australia | 25 | present | straight | 5.5 |
| *M. bispinosa* Hartmann-Schröder, 1960 | Red Sea | 21 | present | straight | 8 |
| *M. nutricula* n.sp. Rouse, 1990 | Australia | 19 | absent | straight | 3.5 |
| *M. jonesi* Kumaraswamy Achari, 1968 | Gulf of Mannar India | 19 | absent | spatulate | 12 |
| *M. ornithochaeta* Mesnil, 1897 | France | 17 | present | spatulate | 4 |
| *M. pamelae* n.sp. Rouse, 1990 | Australia | 23 | absent | straight | 8 |
| *M. rubrospermatheca* n.sp. Rouse, 1990 | Australia | 21 | absent | straight | 3 |

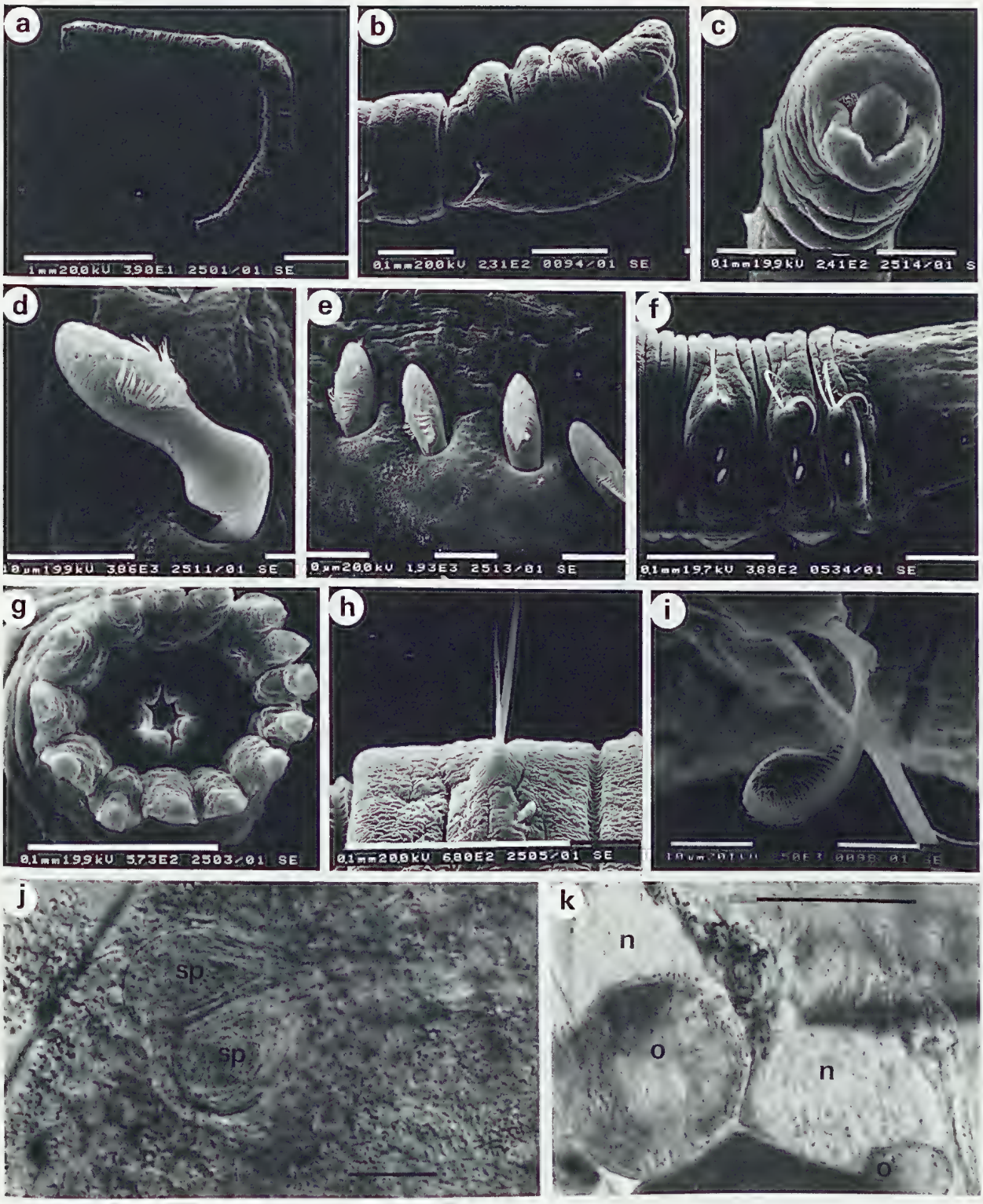


**Fig.2.** *Micromaldane nutricula* n.sp. (AM W 20212): a. S.E.M. side view of whole animal. b. S.E.M. side view of head and anterior setigers. c. S.E.M. frontal view of head showing small nuchal grooves. d. S.E.M. uncini of 7th setiger showing sharp avicular bend. e. S.E.M. uncini of 8th setiger showing four teeth above the main fang and subrostral barbules. f. S.E.M. of posterior end. Note lack of preanal asetigerous segment. g. S.E.M. view of anal plaque showing crenations. h. S.E.M. of 4th setiger. Note lancet type seta and fine capillary seta. i. S.E.M. of 9th setiger showing lancet seta, capillary seta and bifid type geniculate seta. Scale indicated by white bar and bottom left measurement on each figure. *Micromaldane nutricula* n.sp. Holotype (AM W 20210) j. Light micrograph of spermathecae between setigers 10 and 11. Note separate sacs (sp), containing sperm, and ducts leading to the exterior bound together by connective tissue. Scale indicated by black bar 50 µm. k. Light micrograph of vitellogenic oocytes in coelom. Note nurse cells (n) attached at one end of each oocyte (o). Scale indicated by black bar 50 µm.

with 19 setigers and total length of 3.5 mm. Figure 2a shows a mature female with 18 setigers.

Head and anterior 5 setigers red, remainder of body white. 2 clusters of eyespots in front of buccal opening. Nuchal grooves reduced to 2 small furrows (Fig.2c). Head simple, unmodified (Fig.2a,b,c).

Notosetae of 3 types: straight, stout, lancet-shaped setae (Figs 2b,h, 5c), fine bordered capillaries (Figs 2h,i, 5d), or delicate geniculate setae with fine teeth along one margin (Figs 2i, 5e). Only lancet setae and fine capillary setae in notopodia of setigers 1–7 (Fig.2h). After setiger 7 geniculate setae in addition to lancet setae and bordered capillaries. First serration of geniculate setae prominent, giving a bifid appearance (Fig.2i). Fine capillary notosetae absent from posterior setigers. All setigers have 1–3 lancet setae. Fine capillary notosetae present from setigers 1–10 and, after setiger 7, 1–3 geniculate setae. Uncini of neuropodia always lie in single row on all setigers. Setigers 1–7 have 1 or 2 uncini. Setigers 8–14 have 4–6 uncini.

Setigers 15–19 have 3–1 uncini. All uncini strongly curved with a long stem and a prominent main fang with subrostral barbules (Fig.2d). Above main fang are 4 smaller teeth and numerous fine lateral teeth (Fig.2e).

Setigers of midregion of body (8–11) much longer than anterior and posterior setigers (Fig.2a). Preanal asetigerous segment absent. Anal plaque bears no cirri but is sharply crenated 14 times (Fig.2g).

Holotype has 2 pairs of spermathecae attached to body wall with openings on ventral part of body. Spermathecae lie between junctions of setigers 10–11, 11–12. In life spermathecae could be seen through body wall with a compound light microscope (Fig.2j). Ducts leading from spermathecal openings lead into separate sacs bound by connective tissue. Both ducts and sacs contain sperm. No openings from spermathecae into coelomic cavity (Fig.2j). Further details on reproduction in this and other species of *Micromaldane* will be published separately (Rouse, in preparation).

Tube housing holotype, composed of mucous and small particles of siliceous sediment, also contained 5 directly developing larvae. Larvae white in colour. 2 larvae at early stage of development and without setigers; remaining 3 at late stage of development. Body of holotype with large number of white oocytes in coelomic cavity. During oogenesis oocytes float free in coelom. Oocytes have a group of nurse cells attached to one end until end of vitellogenesis (Fig.2k).

**Variation.** The maximum number of setigers appears to be 19. Males lack spermathecae and the body cavity is filled with spermatozoa especially in the posterior region. Most specimens have 16 to 18 setigers and, if female, have broods of larvae. This indicates that sexual maturity is reached before the full complement of setigers is acquired. Where broods were found there were almost always two sets of larvae at different stages of development. All specimens have reddish colouration on the head and the anterior setigers and the remaining part of the body white. Paratypes have similar setal counts to the holotype. Paratype size range from 2 mm to 3.5 mm in length.

**Comments.** *Micromaldane nutricula* n.sp. is similar to *M. jonesi* Kumaraswamy Achari, 1968 in having maximally 19 setigers, no preanal segment and having geniculate setae with a bifid appearance. However *M. nutricula* n.sp. differs from *M. jonesi* in that it has straight lancet-type notosetae instead of spatulate lancet notosetae and is only 3.5 mm long compared to 12 mm. Of the other species of *Micromaldane* only *M. rubrospermatheca* n.sp. has geniculate notosetae with a bifid appearance. *Micromaldane nutricula* n.sp. is clearly distinguishable from the other species described in this study in having oocytes with nurse cells attached, two pairs of spermathecae between setigers 10 and 11 and 11 and 12, and by the ability to have two broods of larvae in the tube at one time.

**Habitat.** Found, gravid all year round, amongst mats of the red algae *Corallina officianilis* in the littoral zone.

**Distribution.** Type locality only.

**Etymology.** Specific name from the latin *nutricula* meaning nurse because of the nurse cells attached to the oocytes.

### *Micromaldane pamelae* n.sp.

Figs 3a–l, 5f–h

**Material examined.** HOLOTYPE: New South Wales, North Bondi rocks, 33°58'S 151°00'E, intertidal, (AM W 20213). PARATYPES: New South Wales, North Bondi rocks, 33°58'S 151°00'E, intertidal, 4 (AM W 20214, in 70% alcohol), 2 (AM W 20215, on S.E.M. stub), 4 (BMNH ZB 1990. 12-15), 4 (HZM P-20210), 4 (USNM). All collected 10 Oct. 1988 by the author.

**Description.** Holotype a complete mature female with 23 setigers and total length of 8 mm. Fig. 3a shows a mature female paratype of 22 setigers.

Head and anterior 5 setigers red, remainder of body white. Prostomium with slight thickening around dorsal edge (Fig.3b). Simple buccal opening ventrally (Fig.3b). 2 clusters of eyespots in front of buccal opening. Nuchal grooves straight (Fig.3c).

Notosetae of 3 types: straight, stout, lancet-shaped setae (Figs 3b,e,f, 5f), fine, bordered capillary setae (Figs 3e,f, 5h), or geniculate setae (Figs 3f, 5g). Setigers 1–10 have 2 or 3 lancet-shaped setae and 2 or 3 fine capillary setae. Setigers 11–23 have 1 or 2 lancet-shaped setae, 1 or 2 capillary setae and 2-6 geniculate setae. Uncini of neuropodia lie in single row on all setigers (Fig.3a,e). Setigers 1–7 have between 2 and 7 uncini. Setigers 8–13 have 10–15 uncini. Setigers 14–19 have 9–6 uncini and setigers 20–23 have from 4 uncini to 1 uncinus. Uncini strongly curved with long shafts and a prominent main fang surrounded by subrostral barbules. 4 smaller teeth and numerous lateral teeth lie over main fang (Fig.3g).

Preanal asetigerous segment absent. Anal plaque bears

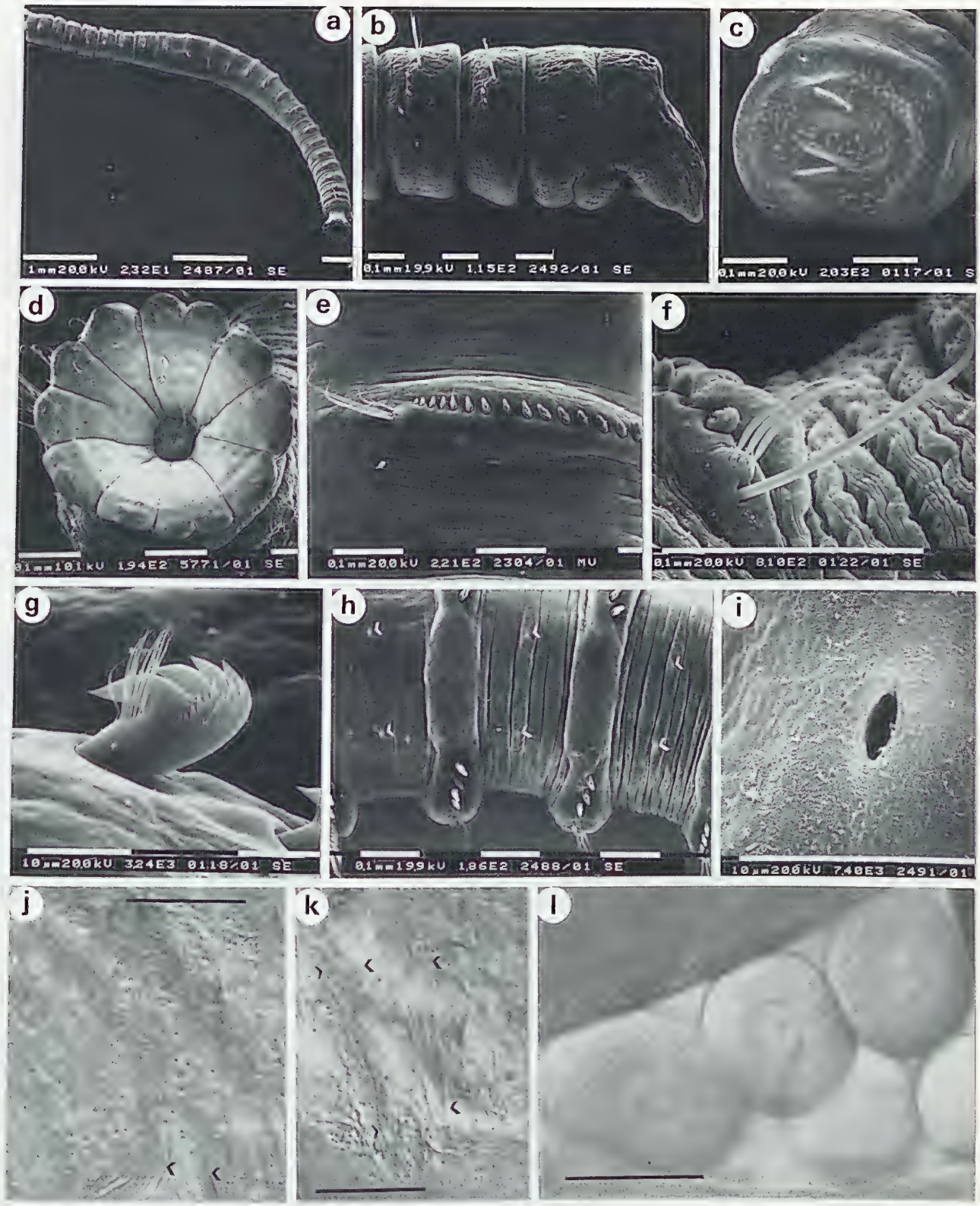


**Fig.3.** *Micromaldane pamelae* n.sp. (AM W 20215): a. S.E.M. oblique dorsal view of whole animal. b. S.E.M. side view of head and anterior setigers. c. S.E.M. frontal view of prostomium. d. S.E.M. view of anal plaque and anus. e. S.E.M. 10th parapodium showing lancet and fine capillary notosetae and single row of neuro-uncini. f. S.E.M. showing 13th setiger showing three types of notosetae. g. S.E.M. side view of uncinus showing main fang, subrostral barbules, four minor teeth over main fang and small lateral teeth. h. S.E.M. ventral of female showing spermathecal entrances (arrows). i. S.E.M. view of a spermathecal opening. Scale indicated by white bar and bottom left measurement on each figure. *Micromaldane pamelae* n.sp. Holotype (AM W 20213) j. Light micrograph of spermathecae showing contained sperm (arrows) between setigers 10–11. Scale indicated by black bar 50 µm. k. Light micrograph of ducts and spermathecal sacs (arrows) between setigers 10–11. Scale indicated by black bar 40 µm. l. Light micrograph of early vitellogenic oocytes. Note absence of nurse cells. Scale indicated by black bar 40 µm.

no cirri but has 12 rounded crenations. Anus lies in middle of anal plaque (Fig.3c). Body divided into 3 distinct regions based on relative size of setigers and development of parapodia. Anterior 6 setigers small and distinct with parapodia relatively undeveloped (Fig.3a,b). Parapodia in middle of segment in anterior setigers (Fig.3a). Setigers 7–12 large and junction between setigers indistinct. Parapodia of these segments show increasing differentiation from rest of segment (Fig.3a,e,i). After setiger 12 segments progressively smaller and all parapodia well developed (Fig.3a).

Holotype has 3 pairs of spermathecae attached to body wall with openings on ventral part of body. Spermathecae lie between junctions of setigers 10–11, 11–12 and 12–13 (Fig.3h). Openings to spermathecae small (less than 5 µm across) and are best seen via the S.E.M. (Fig.3i). In life spermathecae could be seen through body wall with a compound light microscope. Ducts from elliptical spermathecal openings lead into separate sacs bound by connective tissue. Both ducts and sacs contain sperm. No openings from spermathecae into coelomic cavity.

Tube housing holotype, composed of mucous and small particles of siliceous sediment, contained 31 directly developing larvae all at same stage of development and whitish in colour. Body of holotype also contains large number of white oocytes. Oogenesis solitary with oocytes floating free in coelom during vitellogenesis (Fig.3l).

**Variation.** The maximum number of setigers appears to be 23. Males lack spermathecae and the body cavity is filled with spermatozoa. Most specimens had 20 to 22 setigers and, if female, had broods of larvae. This indicates that sexual maturity is reached before the full complement of setigers is acquired. The size of the broods varied from 10 to 31. Setal counts of the paratypes are similar to the holotype. Paratype size range from 6 mm to 8 mm in length. The colour pattern of the anterior region of the body is quite variable. While most specimens have a red anterior, as with the holotype, others may have longitudinal crimson stripes or transverse brown stripes on a cream background or have no colouration at all. This variation does not appear to be sex-linked.

**Comments.** This species can be clearly separated from other species of *Micromaldane* previously described in having a maximum of 23 setigers (see Table 1). Also *M. ornithochaeta* Mesnil, 1897 and *M. jonesi* Kumaraswamy Achari, 1968 have spatulate lancet notosetae (Fig.5l), in contrast to the straight lancet notosetae of *M. pamelae* n.sp. *Micromaldane bispinosa* Hartmann-Schröder, 1960 has straight lancet notosetae, however it differs from *M. pamelae* n.sp. in having fewer setigers and a preanal asetigerous segment. *Micromaldane bispinosa* is also unique in having two types of uncini. *Micromaldane pamelae* n.sp. is clearly different from the three other species described here in overall size, the number of setigers and the shape of the anal plaque although *M. rubrospermatheca* n.sp. is similar in bearing spermathecae between setigers 10 and 11, 11 and 12 and 12 and 13, and in having solitary oogenesis.

**Habitat.** Found, gravid all year round, amongst mats of the red algae *Corallina officianilis* in the littoral zone.

**Distribution.** Type locality only.

**Etymology.** Specific name after Ms Pamela Scott, co-discoverer of this species.

### *Micromaldane rubrospermatheca* n.sp.

Figs4a–l,5i–k

**Material examined.** HOLOTYPE: Queensland, Great Barrier Reef, One Tree Island Reef, 23°30'S 152°05'E (AM W 20216). PARATYPES: Queensland, Great Barrier Reef, One Tree Island Reef, 23°30'S 152°05'E. 8 (AM W 20217, in 70% alcohol), 2 complete and 1 posterior fragment (AM W 20218, on the S.E.M. stub). All collected 2 Dec. 1988 by the author.

**Description.** Holotype a complete mature female with 21 setigers and total length of 3 mm. Fig. 4a shows mature female with 20 setigers.

In life holotype transparent with internal organs clearly visible. After preservation body became uniform white colour. 2 clusters of eyespots in front of buccal opening. Nuchal grooves reduced and head unmodified (Fig.4a,b,c).

Notosetae of 3 types: straight, stout, lancet-shaped setae (Figs 4e,f, 5i), fine bordered capillary setae (Figs 4e, 5k), or delicate geniculate setae with fine teeth along one margin (Figs 4f, 5j). All setigers have 1 lancet-shaped setae. 1 or 2 fine capillary setae on setigers 1–10. Setigers 11–13 have 1 or 2 capillary setae and 1 or 2 geniculate setae. 1 or 2 geniculate setae found along with lancet setae on remaining setigers. First serration of geniculate setae prominent, giving bifid appearance (Fig.4f). Fine capillary notosetae absent from posterior setigers. Uncini of neuropodia lie in single row on all setigers (Fig.4g,h,j). Setigers 1 to 9 have between 1 and 3 uncini. Setigers 10–12 have 4 or 5 uncini. Setigers 13–21 have 3–1 uncini. All uncini avicular with a long stem and prominent main fang bordered with subrostral barbules (Fig.4g,h,i). 4 smaller teeth and numerous fine lateral teeth above main fang (Fig.4g,h,i).

Preanal asetigerous segment absent (Fig.4d). Anal plaque bears no cirri but is slightly crenated (Fig.4d). Anterior setigers bear parapodia in middle of segment (Fig.4c), however segment boundaries difficult to determine in middle and posterior setigers. Setigers of middle region of body (10–13) much longer than the rest (Fig.4a).

Holotype has 3 pairs of spermathecae attached to body wall with openings on ventral part of body. Spermathecae lie between junctions of setigers 10–11, 11–12 and 12–13

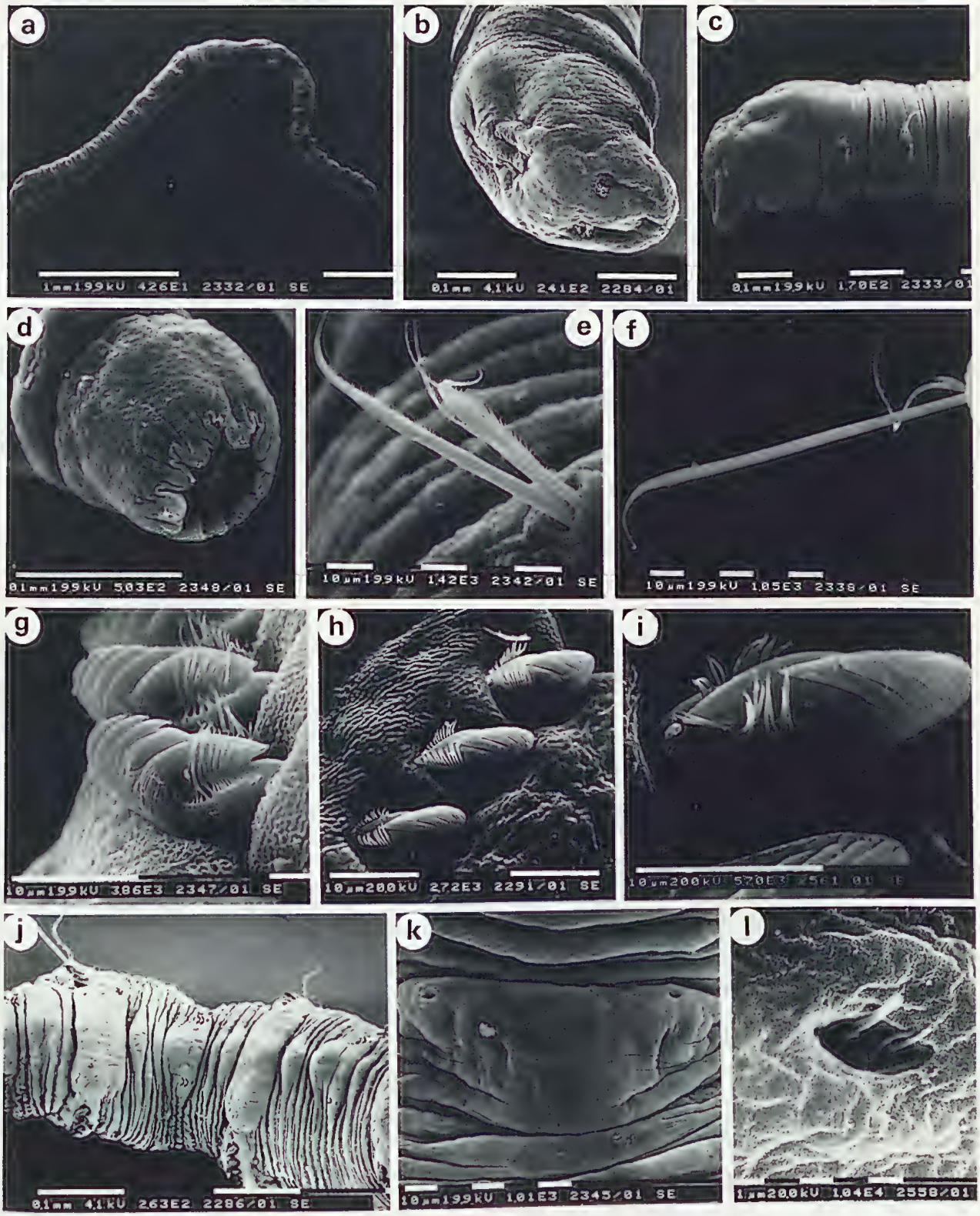


**Fig.4.** *Micromaldane rubrospermatheca* n.sp. (AM W 20218): a. S.E.M. side view of whole animal. b. S.E.M. frontal view of head showing small nuchal grooves. c. S.E.M. side view of head and anterior setigers. d. S.E.M. view of anal plaque showing slight crenations. e. S.E.M. view of notopodium of 6th setiger showing lancet setae and bordered capillary setae. f. S.E.M. view of notopodium of 14th setiger showing lancet setae and bifid type geniculate setae. g. S.E.M. showing side view of uncini with main fang, subrostral barbules, four minor teeth over main fang and small lateral teeth. h. S.E.M. showing single row of uncini of 7th setiger. i. S.E.M. of single uncinus showing main fang, subrostral barbules, four minor teeth over main fang and small lateral teeth. j. S.E.M. ventral of female showing spermathecal entrances of setigers 10–11, 11–12, 12–13 (arrows). k. S.E.M. view of a spermathecal openings of setiger 11–12. l. S.E.M. view of spermathecal opening of setigers 10–11. Note possible spermatozoa in the opening. Scale indicated by white bar and bottom left measurement on each figure.

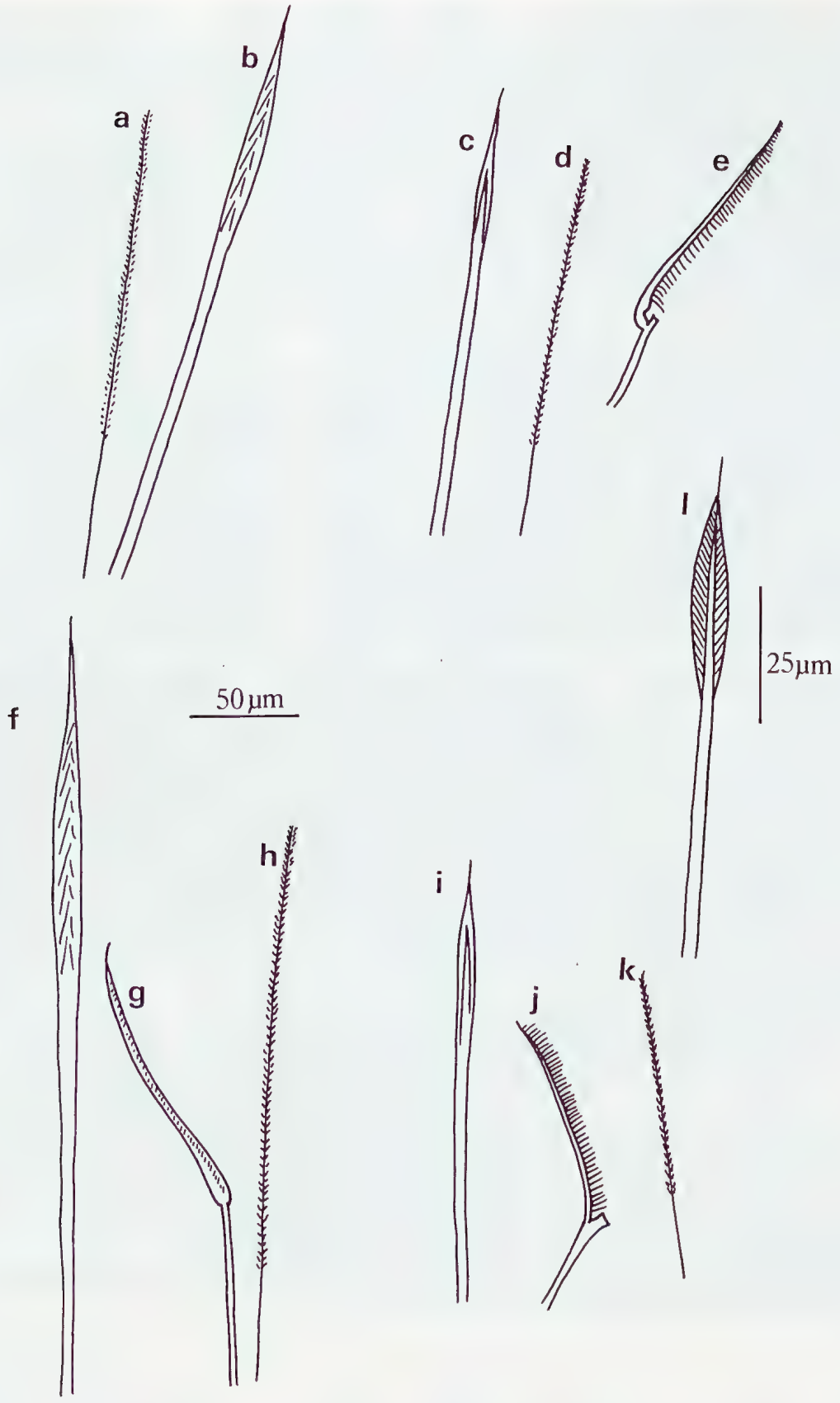


**Fig.5.** *Micromaldane androgyne* n.sp. paratype (AM W 20208): a. Fine capillary notoseta. b. Lancet type notoseta. *Micromaldane nutricula* n.sp. paratype (AM W 20211): c. Lancet type notoseta. d. Fine capillary notoseta. e. Geniculate notoseta. *Micromaldane pamelae* n.sp. paratype (AM W 20214): f. Lancet type notoseta. g. Geniculate notoseta. h. Fine capillary notoseta. *Micromaldane rubrospermatheca* n.sp. paratype (AM W 20217) i. Lancet type notoseta. j. Geniculate notoseta. k. Fine capillary notoseta. Scale bar for 5 a-k 50 µm. *Micromaldane ornithochaeta* Mesnil: l. Spatulate notoseta redrawn from Mesnil (1897). Scale bar 25 µm.

(Fig.4j). Elliptical openings to spermathecae small (5 µm across) and best seen via the S.E.M (Fig.4j,k,l). In life spermathecae could be seen through body wall with compound lightmicroscope. Ducts leading from spermathecal openings lead into separate sacs bound by connective tissue. Both ducts and sacs contain sperm. No openings from spermathecae into coelomic cavity. Connective tissue surrounding spermathecae was bright red in life and still visible in preserved specimen.

Tube housing holotype, composed of mucous and small particles of calcium carbonate sediment, also contained 8 directly developing larvae all at same stage of development and whitish in colour. Body of holotype also has similar number of white oocytes in coelomic cavity. Oogenesis solitary with oocytes floating free in coelom during vitellogenesis.

**Variation.** The maximum number of setigers appears to be 21. Males lack spermathecae and the body cavity is filled with spermatozoa. Most specimens have 19 to 20 setigers and, if female, have broods of larvae. This indicates that sexual maturity is reached before the full complement of setigers is acquired. The colour pattern of the anterior region of the body is variable with some specimens having small red spots in the middle of the prostomium whereas most, like the holotype, were transparent. Setal counts for paratypes are similar to that of the holotype. Paratypes range from 2.5 to 3mm in length.

**Comments.** Of the previously described species of *Micromaldane* only *M. bispinosa* Hartmann-Schröder, 1960 has 21 setigers. *Micromaldane rubrospermatheca* can be clearly distinguished from *M. bispinosa* in being much smaller (see Table 1) and lacking a preanal asetigerous segment. *Micromaldane bispinosa* also has two types of uncini, a feature not found in any other species of *Micromaldane* described to date. Of the other species described in this study *M. rubrospermatheca* n.sp. most closely resembles *M. pamelae* n.sp. in having spermathecae between setigers 10 and 11, 11 and 12 and 12 and 13, and in having solitary oogenesis. However *M. rubrospermatheca* n.sp. is much smaller than *M. pamelae* n.sp. and has fewer setigers, fewer larvae per brood, and distinctive red colouration of the connective tissue around the spermathecae.

**Habitat.** Found intertidally, gravid all year round, among mats of the red algae *Laurencia* sp. on the upper reef crest on the north-eastern side of One Tree Reef.

**Distribution.** Type locality only.

**Etymology.** Derived from the latin *rubor* meaning red, and *spermathecae* meaning sperm case.

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# New Species of *Oriopsis* and a New Record for *Augeneriella* cf. *dubia* Hartmann-Schröder, 1965 from Eastern Australia (Polychaeta: Sabellidae)

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ABSTRACT. Some species of *Oriopsis* found around the rocky shores of Sydney, Australia are described and a key to Australian species is provided. Four new species are described: *Oriopsis bicoloris* n.sp., *O. brevicollaris* n.sp., *O. dentata* n.sp. and *O. mobilis* n.sp. *Augeneriella* cf. *dubia* Hartmann-Schröder, previously known from Hawaii, is recorded from the Great Barrier Reef. The identification of *A.* cf. *dubia* is tentative due to poor type material. The definitions for both genera are discussed and emended.

ROUSE, G.W., 1990. New species of *Oriopsis* and a new record for *Augeneriella* cf. *dubia* Hartmann-Schröder, 1965 from eastern Australia (Polychaeta: Sabellidae). Records of the Australian Museum 42(2): 221–235.

The few records of the sabellid sub-family Fabricinae made in Australia prior to 1979 have been listed by Day & Hutchings (1979). *Oriopsis michaelseni* Banse,1957 was described from Western Australia and additional new species have been described from Western Australia (*O. busseltonensis* Hartmann-Schröder, 1982) and South Australia (*O. cincta* Hartmann-Schröder, 1986 and *O. denticollis* Hartmann-Schröder, 1986). The two records of *Oriopsis* species found in eastern Australian waters, *O.* cf. *michaelseni* Banse, 1957 and *O. parvula* (Ehlers, 1913), are doubtful (see Banse, 1957). No records of fabriciin sabellids have been made from the Great Barrier Reef to date. Examination of rocky intertidal areas on the eastern Australian coast (New South Wales) has revealed four new species of *Oriopsis*. *Augeneriella* cf. *dubia* Hartmann-Schröder, 1965, previously known only from the type locality of Hawaii, is recorded and described from One Tree Reef, Great Barrier Reef.

Little use has been made of scanning electron microscopy (S.E.M.) in the taxonomy of small sabellids. Ben Eliahu (1975) and Wu (1984) have examined *Oriopsis* species with S.E.M. and in the following descriptions it is clear that this form of examination is invaluable with animals of such small size.

## Materials and Methods

Collections of algal mats, sediment and encrustations were made from the lower intertidal zone at the sites indicated in the text. This material was then sorted under a binocular microscope. All species described here are tubiculous but readily leave the tube upon being disturbed and are easily seen. Specimens of all species were examined alive before fixation in 10% sea-water formalin and transfered to 70% ethanol (after washing). Photomicrographs were taken with a Leitz Dialux photomicroscope using Interference Contrast and an Orthomat camera. For S.E.M., specimens were dehydrated in ethanol, cleaned by ultrasonication, and critical point dried with $CO^2$ and coated with gold or platinum (200Å) before viewing with a Philips 505 S.E.M. Descriptions of new species are based on the alcohol preserved holotype and some S.E.M. observations of paratypes, and the variation is based on alcohol preserved paratypes.

The following abbreviations have been used: AHF – Allan Hancock Foundation, Los Angeles; AM – Australian Museum, Sydney; AMNH – American Museum of Natural History; BMNH – British Museum of Natural History, London; HZM – Zoologisches Institut und Zoologisches Museum der Universität, Hamburg; USNM – National Museum of Natural History, Smithsonian Institution, Washington D.C.; ZMC – Zoologisches Museum, Copenhagen.

## Systematics

### Fabricinae Rioja

Fabricinae Rioja, 1923: 13.—Banse, 1957: 97–99.—Fauchald, 1977: 136.

**Diagnosis.** Sabellidae with no companion setae in thoracic segments. Acicular uncini in thoracic neuropodia.

### *Oriopsis* Caullery & Mesnil, emended

*Oriopsis* Caullery & Mesnil, 1896: 483–484, figs 1–2.—Banse, 1957: 68–69, fig. 1.—Fauchald, 1977: 139.—Knight-Jones, 1983: 289–290.
*Oria* Quatrefages, 1866: 462
*Oriades* Chamberlin, 1919: 470.
*Oridia* Rioja, 1917: 73.

**Type species.** *Fabricia armandi* Claparède, 1864, designated by Banse, 1957.

**Diagnosis.** Fabricinae with 3–5 pairs of radioles, without eyes or ridges. Radioles with external flanges. Branchial hearts absent. 1 or 2 pairs of filaments arise from between ventral halves of radiolar crown. Collar may be present or absent; when present is incomplete, forming a gap dorsally. Usually a pair of eyes in collar segment and a pair of statocysts in first setiger. Pair of eyes present in pygidium. Body comprised of 8 thoracic and more than 4 abdominal setigers. First thoracic setiger bears notosetae only, other setigers biramous. Thoracic notosetae may be long or short, limbate or sub-spatulate/spatulate capillaries and, in some species, short, bayonet setae. Thoracic neurosetae, generally few in number, are acicular uncini with a prominent basal tooth and 2–3 arcs of teeth above it, with teeth of first arc fewer and stouter than those of upper arcs. Abdominal uncini usually quadrangular, avicular, toothed margin usually more or less parallel to base and usually with well-defined notch at anterior margin. Abdominal neurosetae a few long capillaries, sometimes limbate, arranged in clusters of 2 or 3. Glandular areas are indistinct, may be visible ventrally as shields, each divided by a transverse groove.

**Comments.** This diagnosis is slightly modified from that of Knight-Jones (1983). The definition of number of abdominal segments has been altered. Knight-Jones (1983) stated "...abdominal setigers fewer than those of the thorax but not less than four..." however, *O. alatoides* Hartmann-Schröder, 1962, *O. bansei* Day, 1961, *O. crenicollis* (Annenkova, 1934), *O. eimeri* (Langerhans, 1880), *O. magellanica* Hartmann-Schröder, 1962 and *O. rivularis* (Annenkova, 1929) all have more abdominal setigers than those of the thorax (Table 1).

Bayonet setae have only been recorded in the type species *O. armandi* (by Fauvel, 1927) and in *O. rivularis*. These setae are characteristic of the genus *Chone* (see Banse, 1972) but have also been found in three of the new species described here. They are difficult to distinguish with the light microscope but are easily seen with the S.E.M. Closer examination of other species may reveal a wider distribution of these setae.

The absence of a glandular girdle as a character is removed due to the fact that *O. cincta* Hartmann-Schröder, 1986 and all four new species described in this paper have a glandular girdle around the second setiger. Other genera of the Fabricinae e.g. *Euchone* Malmgren, 1866, *Chone* Krøyer, 1856, *Jasmineira* Langerhans, 1880 have this feature (see Banse, 1972) and it may well have been overlooked in animals of the very small size typical of *Oriopsis*. Banse (1972) states that some species of Oriopsis, e.g. *O. rivularis*, can only be excluded from the genus *Chone* on the basis that they lack the glandular girdle. Examination of all species in *Chone* and *Oriopsis* is needed to properly define the characters distinguishing the two genera.

The filaments lying between the halves of the radiolar crown are functionally different to the pinnules of the radioles and appear to be involved in tube construction. They are mobile and often in contact with the substrate (personal observations on live material). Day (1967) suggests they simulate the palps of other polychaetes. Since it has not been proved they are homologous with palps they will here be termed filaments to distinguish them from the pinnules of the radioles.

Table 1. Distinguishing features of *Oriopsis*.

| Species and subspecies | Radioles (pairs) | Abd. setigers | Filaments (pairs) | Collar | Thoracic notosetae | Type locality |
|---|---|---|---|---|---|---|
| *O. alata* (Ehlers, 1897) | 4 | 6 | 1 | absent | limbate | South Georgia |
| *O. alata pectinata* Banse, 1957 | 4 | 6 | 2 | vestigial | bilimbate | New Zealand |
| *O. alatoides* Hartmann-Schröder, 1962 | 3 | 11 | 1 | lateral clefts | bilimbate | Chile |
| *O. armandi* (Claparède, 1864) | 3 | 4-12 | 1 | smooth | subspatulate | Mediterranean |
| *O. bansei* Day, 1961 | 3-4 | 9 | 1 | smooth | subspatulate | South Africa |
| *O. bicoloris* n.sp. Rouse, 1990 | 3 | 9 | 2 | smooth | limbate | NSW, Australia |
| *O. brevicollaris* n.sp. Rouse, 1990 | 4 | 7 | 2 | vestigial | bilimbate | NSW, Australia |
| *O. busseltonensis* Hartmann-Schröder, 1982 | 4 | 6 | 1 | crenulate | bilimbate | WA, Australia |
| *O. cincta* Hartmann-Schröder, 1986 | 4 | 8 | 0? | irregular crenations | bilimbate | SA, Australia |
| *O. coalescens* Banse, 1959 | 4 | 6 | 1 | ventral projection | bilimbate | South India |
| *O. crenicollis* (Annenkova, 1934) | 3-4 | 15 | ? | crenulate | spatulate | Bering Strait |
| *O. dentata* n.sp. Rouse, 1990 | 3 | 11 | 2 | smooth ventral notch | spatulate | NSW, Australia |
| *O. denticollis* Hartmann-Schröder, 1986 | 4 | 6 | 2 | crenulate | bilimbate | SA, Australia |
| *O. ehlersi* Day, 1961 | 3 | 7 | 2 | smooth ventral notch | subspatulate | South Africa |
| *O. eimeri* (Langerhans, 1880) | 3 | 9-10 | 1? | crenulate | subspatulate | Madeira |
| *O. eimeri australis* Hartmann-Schröder, 1981 | 4 | 8 | 0 | crenulate | spatulate | WA, Australia |
| *O. eimeri persinosa* Ben-Eliahu, 1975 | 5 | 10 | ? | crenulate | limbate | Mediterranean |
| *O. gracilis* Hartman, 1969 | 3 | 8 | 0? | absent or vestigial | bilimbate | California, USA |
| *O. hynensis* Knight-Jones, 1983 | 3 | 5 | 1 | wide dorsal gap | bilimbate | Ireland |
| *O. limbata* (Ehlers, 1897) | 4 | 5 | 1 | ventral notch and projection | limbate | South Patagonia |
| *O. magellanica* Hartmann-Schröder, 1962 | 4 | 9 | ? | smooth ventral notch | bilimbate | Chile |
| *O. magna* Banse, 1957 | 5 | 5 | 1 | smooth ventral notch | bilimbate | South Georgia |
| *O. michaelseni* Banse, 1957 | 4-5 | 6 | 1 | dorsal gap vent. projection | bilimbate | WA, Australia |
| *O. minuta* (Berkeley & Berkeley, 1932) | 2 | 5 | ? | absent | spatulate | Canada |
| *O. mobilis* n.sp. Rouse, 1990 | 3 | 5 | 1 | smooth ventral notch | limbate | NSW, Australia |
| *O. neglecta* Banse, 1957 | 4 | 5-6 | 1 | absent | subspatulate | South Africa |
| *O. pacifica* (Rullier, 1977) | 3 | 3 | ? | absent? | bilimbate | New Caledonia |
| *O. parvula* (Ehlers, 1913) | 3 | 6 | 1 | ventral projection | straight capillaries | South Africa |
| *O. rivularis* (Annenkova, 1929) | 3 | 17 | 1 | absent | spatulate | Sea of Ohktosk |
| *O. taltanensis* Hartmann-Schröder, 1962 | 3 | 5 | 1 | dorsal clefts | bilimbate | Chile |
| *O. tristanenesis* (Day, 1954) | 4 | 6 | 0? | crenulate | spatulate | Tristan da Cuhna |

The number of abdominal setigers and radioles in the crown (Day, 1961) and the structure of the collar (Knight-Jones, 1983) are regarded as good specific characters for *Oriopsis*. These features are summarised in Table 1. The number of abdominal setigers ascribed to some species of *Oriopsis* is variable (Table 1). However in all four species described here a maximum number of setigers was observed. It appears that adults continue to add abdominal setigers after reaching sexual maturity until they reach this maximum. For previously described species discussed here, the largest number of abdominal segments described by the author will be regarded as the adult number.

Considerable confusion exists over the location of the peristomium in members of the Fabricinae. Several authors, Hartman (1951), Banse (1957) and Day (1967), state that the first body segment bearing the collar and a pair of eyes, when present, is the peristomium. Fitzhugh (1983) regards the segment bearing the collar to be separate from, and posterior to, the peristomium. Knight-Jones (1983) appears to regard the first setiger as the first body segment and so bears the collar and eyes, where present, as well as notosetae. In this study the position of Hartman (1951), Banse (1957) and Day (1967) has been followed although the peristomium may in fact be fused to the first asetigerous body segment.

## Key to the Australian Species of *Oriopsis* *

1. Collar prominent ..... 2

—— Collar vestigial ..... *O. brevicollaris* n.sp.

2. Collar crenulate or irregular ..... 3

—— Collar smooth ..... 6

3. 6 abdominal setigers ..... 4

—— 8 abdominal setigers ..... 5

4. Collar low and irregular ..... *O. busseltonensis*

—— Collar high and evenly crenulate ..... *O. denticollis*

5. Distinct glandular girdle around setiger 2 ..... *O. cincta*

—— Glandular girdle absent or indistinct ..... *O. eimeri australis*

6. 3 pairs of radioles ..... 7

—— More than 3 pairs of radioles ..... *O. michaelseni*

7. 5 abdominal setigers ..... *O. mobilis* n.sp.

—— More than 5 abdominal setigers ..... 8

8. 9 abdominal setigers ..... *O. bicoloris* n.sp.

—— 11 abdominal setigers ..... *O. dentata* n.sp.

*This key is not meant to imply phylogenetic relationships.

### *Oriopsis bicoloris* n.sp.

Figs 1a–i, 2a–b

**Material examined.** HOLOTYPE: New South Wales, Port Jackson, Bottle and Glass rocks, 33°58'S 151°00'E, intertidal, (AM W 203545). PARATYPES: New South Wales, Port Jackson, Bottle and Glass Rocks, 33°58'S 151°00'E, intertidal, 4 (AM W 203550, in 70% alcohol), 4 (AM W 203559, on S.E.M. stub), 4 (AHF POLY 1491), 4 (BMNH ZB 1989.11-14), 4 (HZM P-19693), 4 (USNM 122288). All collected 25 Nov. 1988 by the author.

**Other material examined.** *Oriopsis cincta* Paratype: Australia South Australia, Kangaroo Island (HZM P-18634). Collected 14 Dec. 1975 by G. Hartmann-Schröder.

**Description.** Complete mature female with 8 thoracic and 9 abdominal setigers (Fig.1a). Total length of 2.1 mm. Crown made up of 3 pairs of radioles with distinct lateral flanges (Fig.1b). The flanges fuse above the bases of the radioles forming a slight web (Fig.1a). Each radiole with 5-6 pairs of pinnules ending with a terminal pinnule. Pinnules of each radiole equal in length. 2 pairs of filaments ventrally between halves of crown. Branchial hearts absent. Thoracic collar high, smooth and complete with a distinct notch ventrally. Posterior to notch is a large rectangular ciliated patch. Collar separated dorsally by a narrow gap (Fig.1a). No eyes or statocysts visible in preserved specimen, however in life a pair of red eyes

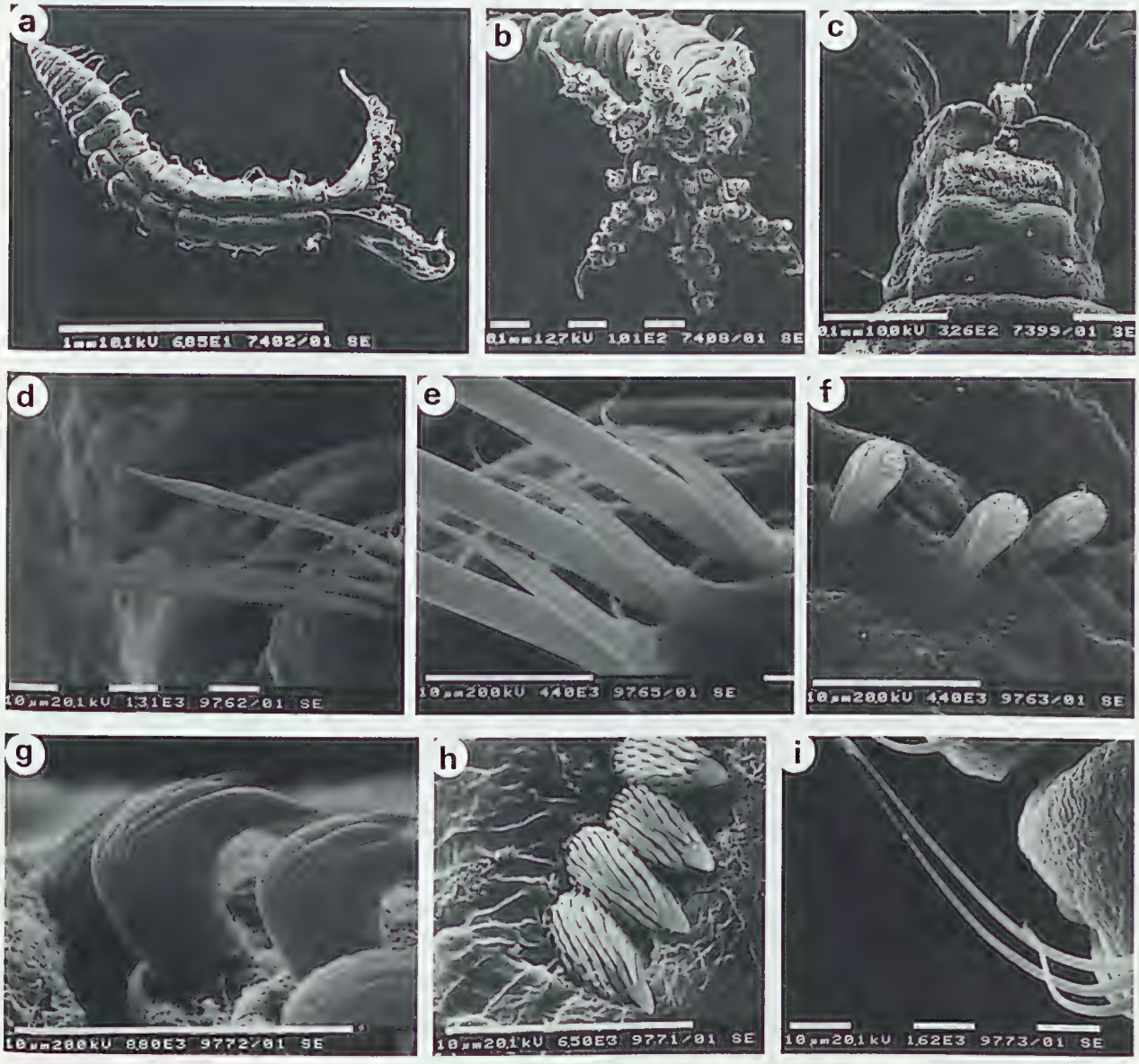


**Fig.1.** *Oriopsis bicoloris* n.sp. (AM W 203557): a. S.E.M. dorsal view of whole animal showing narrow gap in collar. b. S.E.M. frontal view of crown showing three pairs of radioles. Note lateral flanges of radioles. c. S.E.M. view of collar region showing ventral notch and ciliated patch. d. S.E.M. showing long limbate and short bayonet capillary notosetae of thorax. e. S.E.M. showing bayonet notosetae of thorax. f. S.E.M. showing frontal view of thoracic uncini. g. S.E.M. showing side view of thoracic uncini. h. S.E.M. showing abdominal uncini. i. S.E.M. showing capillary neurosetae of abdomen. Scale indicated by white bar and bottom left measurement on each figure.

were apparent in peristomium (Fig.2a) and another in pygidium. A pair of spermathecae visible in collar before preservation (Fig.2a). A pair of statocysts also visible in first setiger (Fig.2a,b). A glandular girdle, immediately behind setae of second setiger, was evident when alive (Fig. 2a) and is visible in preserved holotype.

Thoracic notopodia have 3–4 long, limbate capillaries with fine teeth along one margin and 3–4 short bayonet setae per torus (Fig.1d,e). Thoracic neurosetae acicular uncini with 3 rows of teeth above basal tooth. First row above basal tooth has a large central tooth flanked by smaller teeth (Fig.1f,g). Between 3 and 6 uncini per torus, decreasing in posterior segments. Abdominal uncini quadrangular with distal surface covered with rows of small teeth over a small basal tooth (Fig.1h). Between 4 and 13 uncini per torus. Abdominal neurosetae capillaries, 1–3 per

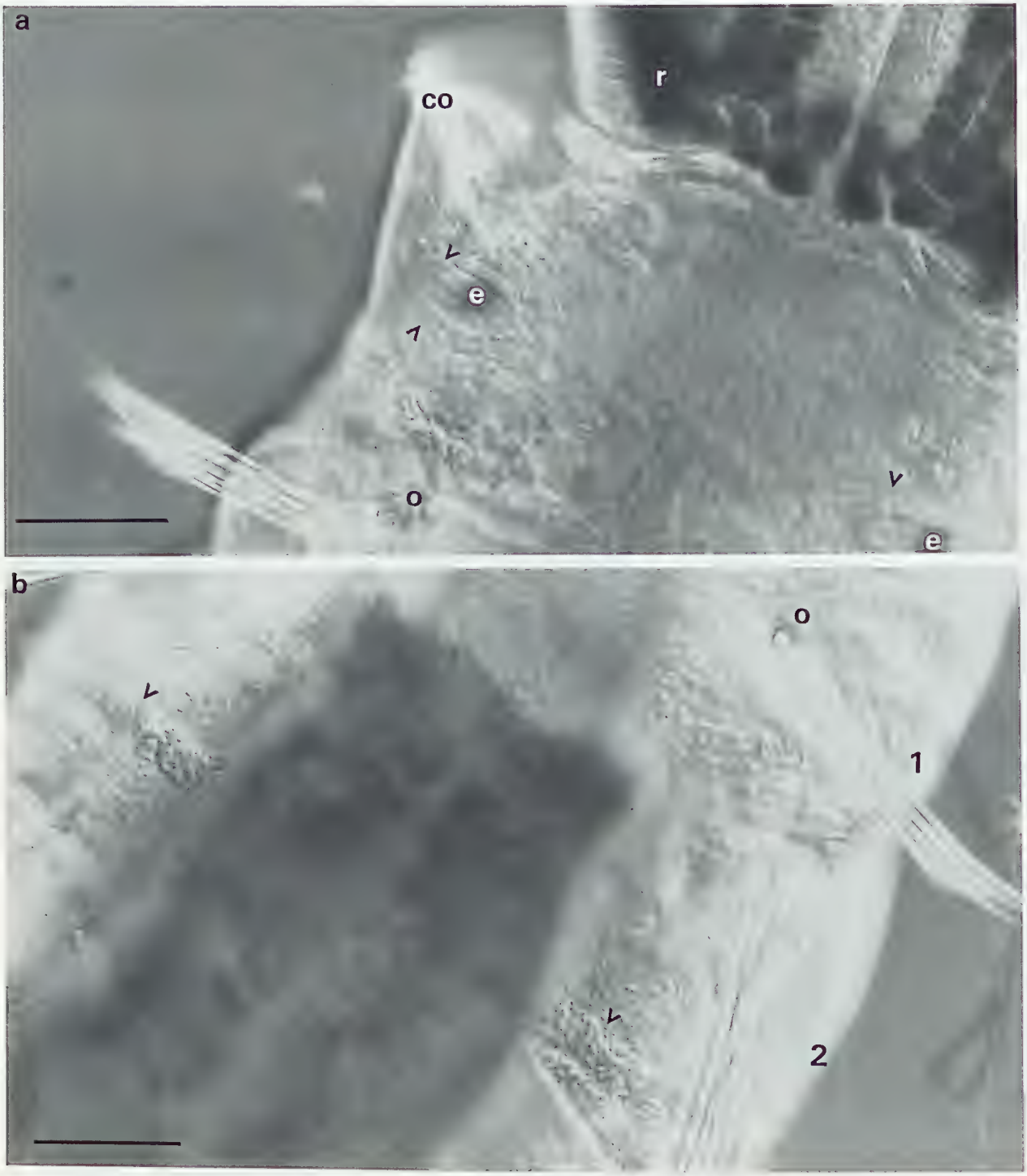


**Fig.2.** *Oriopsis bicoloris* n.sp. holotype (AM W 203551). a. Light micrograph of live holotype showing base of radiolar crown (r), collar (co), eyes (e), spermathecae in collar (indicated by arrows) and statocyst in first setiger (o). b. Light micrograph of live holotype showing statocyst in first setiger (o) and glandular girdle behind the setae of the second setiger (indicated by arrows). Scale bar for both a. and b. is 100 μm.

torus (Fig.1i).

Pygidium semicircular. Faecal groove visible mid-dorsally along thorax (Fig.1a) and midventrally along abdomen to anus. Holotype opaque, uniformly white. In life body was transparent with entire length of radiolar flanges white in colour and orange eggs in posterior thoracic setigers of female. Tube fragile and closely fitting around occupant, composed of fine brown silt and mucous.

**Variation.** The maximum number of abdominal setigers is nine, with smaller, juvenile, specimens having fewer than this number. The paratype material matches that of the holotype very closely. Many specimens showed pink colouration along radioles in life instead of the more common white pigmentation. All paratypes have eight thoracic and seven to nine abdominal setigers. Paratype size range from 1.5 mm to 2 mm in length.

**Comments.** Of the species of *Oriopsis* with three pairs of radioles forming the crown only *Oriopsis bansei* Day, 1961 has nine abdominal segments. *Oriopsis bansei* also has a collar with smooth margins, a ventral notch and a small dorsal gap. However *O. bansei,* from South Africa, may have four pairs of radioles and has thoracic notosetae with characteristic broad blades, not limbate setae, as well as differences in overall setal count from *O. bicoloris* n.sp. No glandular girdle has been recorded for any other species of *Oriopsis* apart from *O. cincta* Hartmann-Schröder, 1986 which has four pairs of radioles and eight abdominal setigers, and the four new species described here. The presence of a glandular girdle around the second setiger was named as an important difference between *Oriopsis* and *Chone* by Banse (1972). *Oriopsis bicoloris* and any of the other new species described here should not be referred to *Chone* since they lack the three types of thoracic notosetae typical of that genus. They also have fewer radioles and abdominal setigers than any species of *Chone* described to date. However, Rouse (in preparation) has found marked differences in sperm structure amongst the four species of *Oriopsis* recorded here and has located spermathecae in females of three of the species. Further investigation of sperm and spermathecae amongst members of the Fabricinae is required to determine the importance of these features taxonomically.

**Habitat.** Found, gravid all year round, forming dense mats of tubes (greater than 250,000 $m^2$) along with an unidentified spionid just below low water spring tide in rock pools.

**Distribution.** Type locality only.

**Etymology.** Specific name is from the latin *bicolor*, meaning two coloured, referring to the white or pink colouring of the radioles.

### *Oriopsis brevicollaris* n.sp.

Fig.3a–i

**Material examined.** HOLOTYPE: New South Wales, North Bondi rocks, 33°58'S 151°00'E, intertidal, (AM W 203553) PARATYPES: New South Wales, North Bondi rocks, 33°58'S 151°00'E, intertidal, 6 (AM W 203554, in 70% alcohol), 3 (AM W 203558, on S.E.M. stub), 6 (AHF POLY 1492), 6 (BMNH ZB 1989.15-20), 6 (HZM P-19694), 6 (USNM 122290). All collected 30 Nov. 1988 by the author.

**Other material examined.** HOLOTYPE: *Oriopsis alata pectinata* Banse, 1957 (ZMC) New Zealand Masked Island, Carnley Harbour. Collected 3 Dec. 1914.

**Description.** Complete mature female with 8 thoracic and 7 abdominal setigers (Fig.3a). Total length 1.8 mm. Crown has 4 pairs of radioles, each with lateral flanges (Fig.3c). Flanges fuse to form a web above bases of radioles (Fig.3a). Each radiole with 7 pairs of pinnules ending with a long terminal pinnule. Main pinnules extend beyond level of terminal pinnule of each radiole. 2 pairs of filaments ventrally between halves of crown. One pair almost length of radioles with second pair shorter and thicker. Branchial hearts absent. Thoracic collar reduced to a thin flange dorsally and laterally, extending forward ventrally to form a triangular projection with a small notch (Fig.3b,c). Collar separated dorsally by a wide gap. Eyes and statocysts not visible in alcohol preserved holotype, however in life it had a pair of red eyes in peristomium and another in pygidium. When alive a pair of statocysts also visible in first setiger. A thin glandular girdle occurs behind setae of second setiger, however this feature difficult to see in preserved holotype.

Thoracic notopodia with 3–4 long bilimbate capillaries and 3–4 short bayonet setae per torus (Fig.3e). Thoracic neurosetae acicular uncini with 3 rows of teeth above basal tooth. First row above basal tooth has a large central tooth only (Fig.3f,g). Between 3 and 6 uncini per torus decreasing in posterior segments. Abdominal notosetae have quadrangular uncini with distal surface covered with rows of small teeth overlying a large basal tooth (Fig.3h). Between 6 and 10 uncini per torus. Abdominal neurosetae simple capillaries, 2–3 per torus (Fig.3i).

Pygidium semicircular. Faecal groove runs along dorsal surface of the animal only. Anus dorsal (Fig.3a). Midthoracic segments are distinctly longer and wider than other segments (Fig.3a). Holotype opaque, uniformly white. In life body transparent and orange eggs visible in thoracic setigers. Tube composed of fine sediment and mucous, 3–4 times length of animal and closely fitting around occupant.

**Variation.** The maximum number of abdominal setigers is seven, with smaller specimens having fewer than this number. The paratype material matches that of the holotype very closely except smaller specimens also have fewer radioles and abdominal setigers. All paratypes

have eight thoracic and three to seven abdominal setigers. Many have three pairs of radioles or three pairs and one extra, giving a total of seven radioles. Paratype size range from 0.8 mm to 1.8 mm in length.

**Comments.** *Oriopsis brevicollaris* n.sp. can be clearly distinguished from other species of *Oriopsis* in possessing four pairs of radioles and seven abdominal setigers. Only *O. ehlersi* Day, 1961 has seven abdominal setigers but is different from *O. brevicollaris* n.sp. in having three pairs of radioles and a distinct smooth collar. However, the description by Banse (1957) of *O. alata pectinata* is similar to *O. brevicollaris* n.sp. in having a reduced collar, four pairs of radioles, two pairs of ventral filaments, bilimbate thoracic notosetae and numerous abdominal uncini with a very prominent basal tooth. The holotype of *O. alata pectinata* has six abdominal setigers and is much larger (4 mm) than any specimen of *O. brevicollaris* n.sp. (maximum 1.8 mm) with seven setigers. *Oriopsis alata pectinata* has segments of more even width along the body unlike the distinctly wider midthoracic segments of *O. brevicollaris* n.sp.

**Habitat.** Found gravid all year round amongst the tubes of the serpulid polychaete *Filograna implexa* in the littoral zone.

**Distribution.** Type locality only.

**Etymology.** Specific name is derived from the latin *brevis*, meaning short or small, and *collar* for collar.

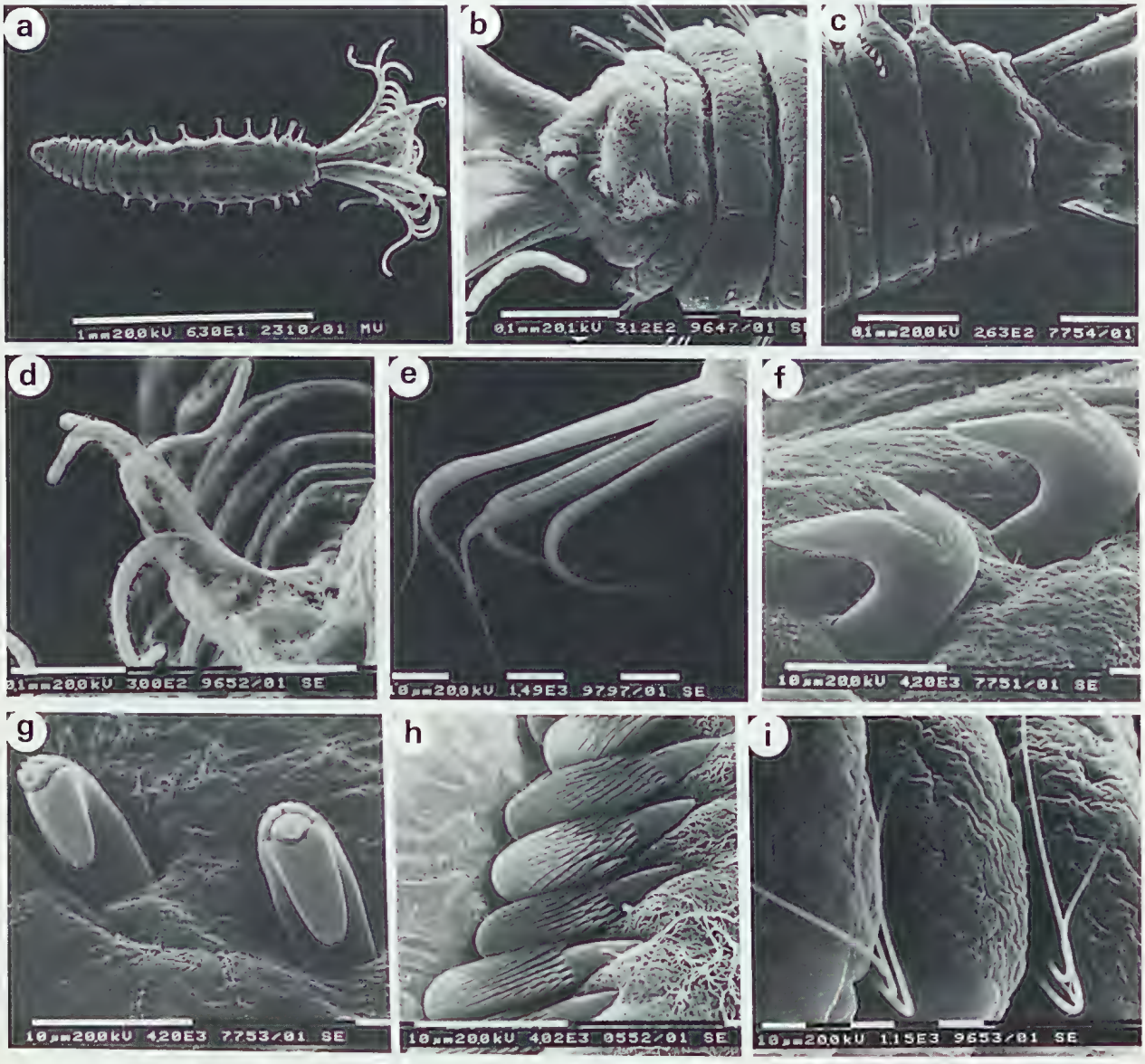


**Fig.3.** *Oriopsis brevicollaris* n.sp. (AM W 203558): a. S.E.M. ventral view of whole animal. b. S.E.M. ventral view of collar region. c. S.E.M. side view of collar region. d. S.E.M. view of one radiole showing lateral flanges characteristic of *Oriopsis*. e. S.E.M. showing long limbate and shorter bayonet notosetae of thorax. f. S.E.M. showing side view of thoracic uncini. g. S.E.M. showing frontal view of thoracic uncini. h. S.E.M. showing abdominal uncini. Note prominent basal teeth. i. S.E.M. showing capillary neurosetae of abdomen. Scale indicated by white bar and bottom left measurement on each figure.

### *Oriopsis dentata* n.sp.

Fig.4a–i

**Material examined.** HOLOTYPE: New South Wales, Port Jackson, Bottle and Glass Rocks, 33°58'S 151°00'E, intertidal, (AM W 203555). PARATYPES: New South Wales, Port Jackson, Bottle and Glass Rocks 33°58'S 151°00'E, intertidal, 5 (AM W 203556, in 70% alcohol), 3 (AM W 203560, on S.E.M. stub), 5 (AHF POLY 1493), 5 (BMNH ZB 1989.21-25), 5 (HZM P-19695), 5 (USNM 122289). All collected 25 Nov. 1988 by the author.

**Description.** Complete mature female with 8 thoracic and 11 abdominal setigers (Fig.4a). Total length of 2.2 mm. Crown of 3 pairs of radioles with distinct lateral flanges (Fig.4b). Flanges fuse above bases of radioles forming a slight web. Each radiole with 6 pairs of pinnules ending with a terminal pinnule. 2 pairs of filaments ventrally between halves of crown. One pair as long as crown, second approximately one quarter length of crown. Branchial hearts absent. Thoracic collar high, smooth and complete (Fig.4b,c) with a small notch ventrally. Collar separated dorsally by a wide gap. No eyes or statocysts visible in preserved specimens, however in life holotype had a pair of red eyes apparent in collar segment and in pygidium. A pair of statocysts also found in first setiger in alive specimens. A thin glandular girdle occurs behind setae of second setiger, however this feature difficult to see in preserved holotype.

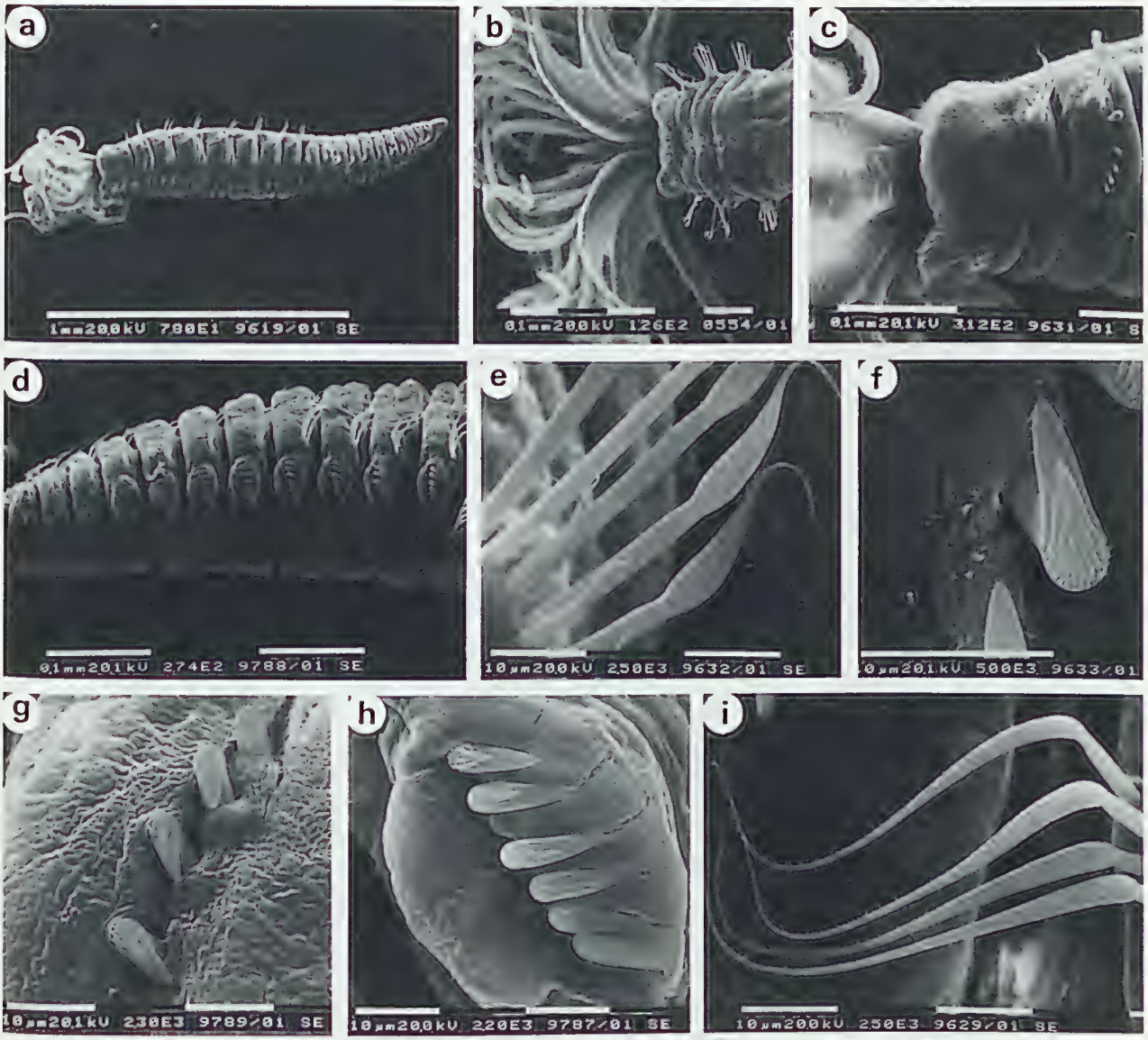


**Fig.4.** *Oriopsis dentata* n.sp. (AM W 203560): a. S.E.M. side view of whole animal. b. S.E.M. dorsal view of crown and collar showing three pairs of radioles and wide gap in collar. Note lateral flanges of radioles fusing to form basal webbing. c. S.E.M. side view of collar region. d. S.E.M. showing abdominal region with 11 setigers. e. S.E.M. showing long spatulate and shorter bayonet notosetae of thorax. f. S.E.M. showing dorsal view of thoracic uncini. g. S.E.M. showing thoracic uncini. h. S.E.M. showing abdominal uncini. Note prominent basal tooth and variation in overlying teeth. i. S.E.M. showing distinct limbate capillary neurosetae of abdomen. Scale indicated by white bar and bottom left measurement on each figure.

Thoracic notosetae 4–5 long spatulate capillaries and 3–4 shorter bayonet setae per torus (Fig.4e). Thoracic neurosetae acicular uncini with 3 rows of teeth above basal tooth. First row above basal tooth has a large central tooth flanked by smaller teeth (Fig.4f,g). Between 2 and 4 uncini per torus, decreasing in posterior segments. Abdominal uncini quadrangular with distal surface covered with rows of small teeth overlying a large basal tooth (Fig.4h). Between 3 and 6 uncini per torus (Fig.4d). Considerable variation in form of rows of teeth overlying basal tooth of abdominal uncini (Fig.4h). Abdominal neurosetae distinct limbate capillaries, 1–4 per torus (Fig.4i).

Pygidium semicircular. Faecal groove runs mid-dorsally along thorax (Fig.4b) and midventrally along abdomen. Holotype opaque, uniformly white. In life body transparent with base of radiolar flanges white in colour and orange eggs in thoracic setigers of females. Tube strong, 3–4 times length of animal, closely fitting around occupant and composed of fine sediment and parchment-like material.

**Variation.** The maximum number of abdominal setigers is eleven, with smaller specimens having fewer than this number. The paratype material matches that of the holotype very closely except for size, and male specimens have body cavity filled with sperm. All paratypes have eight thoracic and four to eleven abdominal setigers. Paratype size range from 0.8 mm to 2.3 mm in length.

**Comments.** Of the species of *Oriopsis* with three pairs of radioles forming the crown only *O. alatoides* Hartmann-Schröder, 1962 has eleven abdominal setigers. It is distinct from *O. dentata* in having only one pair of ventral filaments and ventrolateral clefts in the collar. *Oriopsis crenicollis* (Annenkova, 1934), *O. rivularis* (Annenkova, 1929) and *O. eimeri australis* Hartmann-Schröder, 1981 are similar to *O. dentata* in having spatulate thoracic notosetae, abdominal uncini with a very large basal tooth and limbate abdominal neurosetae, however they have different numbers of abdominal setigers (see Table 1). *Oriopsis dentata*, *O. rivularis* and *O. crenicollis* show some resemblance to small members of the genus *Chone* (see Banse, 1957, 1972) in the form of the abdominal uncini and the limbate abdominal neurosetae. However *O. dentata* cannot currently be referred to *Chone* since it has only two types of thoracic notosetae.

**Habitat.** Found in low numbers amongst dead tubes of the serpulid polychaete *Galeolaria caespitosa*. Also found in low numbers amongst the tubes of the serpulid polychaete *Filograna implexa* in the littoral zone.

**Distribution.** Type locality only.

**Etymology.** Specific name from the latin *dentatus*, meaning toothed, refers to the large basal tooth of the abdominal uncini.

### *Oriopsis mobilis* n.sp.

Fig.5a–i

**Material examined.** HOLOTYPE: New South Wales, North Bondi rocks, 33°58'S 151°00'E, intertidal, (AM W 203545). PARATYPES: New South Wales, North Bondi rocks, 33°58'S 151°00'E, intertidal, 4 (AM W 203550, in 70% alcohol), 4 (AM W 203559, on S.E.M. stub), 4 (AHF POLY 1494), 4 (BMNH ZB 1989.26-29), 4 (HZM P-19696), 4 (USNM 122291). All collected 30 Nov. 1988 by the author.

**Description.** Complete mature female with 8 thoracic and 5 abdominal setigers (Fig.5a). Total length of 1.1 mm. Crown made up of 3 pairs of radioles with distinct lateral flanges (Fig.5b,c). Flanges fuse above bases of radioles forming a slight web (Fig.5c). Each radiole with 5 pairs of pinnules ending with a terminal pinnule. Proximal pinnules of each radiole are longest and extend furthest out giving crown a subspherical appearance (Fig.5a). 2 long filaments ventrally between halves of crown. Branchial hearts absent. Thoracic collar high, smooth and complete with a small notch ventrally (Fig.5e). Posterior to notch is a small ciliated patch. Collar separated dorsally by a small gap (Fig.5d). No eyes or statocysts visible in preserved specimen, however in life holotype had a pair of red eyes in collar segment and another in pygidium. A pair of statocysts also found in first setiger. A thin glandular girdle occurs behind setae of second setiger, however this feature difficult to see in preserved holotype.

Thoracic notosetae limbate capillaries with fine teeth along one margin. Between 3–4 short limbate setae and 3–4 long limbate setae per torus (Fig.5f). Thoracic neurosetae, 3 and 5 acicular uncini per torus, have 2 rows of teeth above basal tooth. First row above basal tooth has a large central tooth flanked by smaller teeth (Fig.5g). Abdominal uncini quadrangular with distal surface covered with rows of small teeth over an indistinct basal tooth (Fig.5h), between 9 and 3 uncini per torus, decreasing posteriorly. Abdominal neurosetae capillaries, 1–2 per torus (Fig.5i).

Pygidium semicircular in shape. Faecal groove arises ventrally from anus and crosses to dorsal side at junction between abdomen and thorax (Fig.5a). Holotype opaque, uniformly white. In life body transparent with white patches at base of crown and orange eggs in posterior thoracic setigers. Tube fragile and closely fitting around occupant, composed of fine brown silt and mucous.

**Variation.** The maximum number of abdominal setigers appears to be five, with smaller specimens having four. The paratype material matches that of the holotype very closely except for size differences and some variation in the white patterns on the radioles. All paratypes have eight thoracic and four or five abdominal setigers. Paratype size range from 0.8 mm to 1.3 mm in length.

**Comments.** Of the previously described species of *Oriopsis* with three pairs of radioles forming the crown, *O. alatoides* Hartmann-Schröder, 1962, *O. ehlersi* Day, 1961, *O. eimeri* (Langerhans, 1880), *O. gracilis* Hartman, 1969, *O. hynensis* Knight-Jones, 1983, *O. rivularis* (Annenkova, 1929) and *O. taltanensis* Hartmann-Schröder, 1962, only *O. taltanensis*, *O. hynensis* and *O. gracilis* have five abdominal setigers. None of these species has a collar with a ventral notch or a small dorsal gap. *Oriopsis taltanensis* has unique dorsal clefts in the collar margin, *O. hynensis* has a very low collar that exposes the peristomium ventrally and has a very wide dorsal gap, *O. gracilis* has no collar or only vestiges of one.

**Habitat.** Found, gravid all year round, amongst mats of the red alga *Corallina officianilis* and the tubes of the serpulid polychaete *Filograna implexa* in the littoral zone.

**Distribution.** Type locality only.

**Etymology.** Specific name is from the latin *mobilis*, meaning nimble, referring to the violent flexing of the body this species undergoes when disturbed.

### *Augeneriella* Banse, emended

*Augeneriella* Banse, 1957: 95–96, fig 9.—Hartmann-Schröder, 1965: 156–158.—Gitay, 1970: 105–109.—

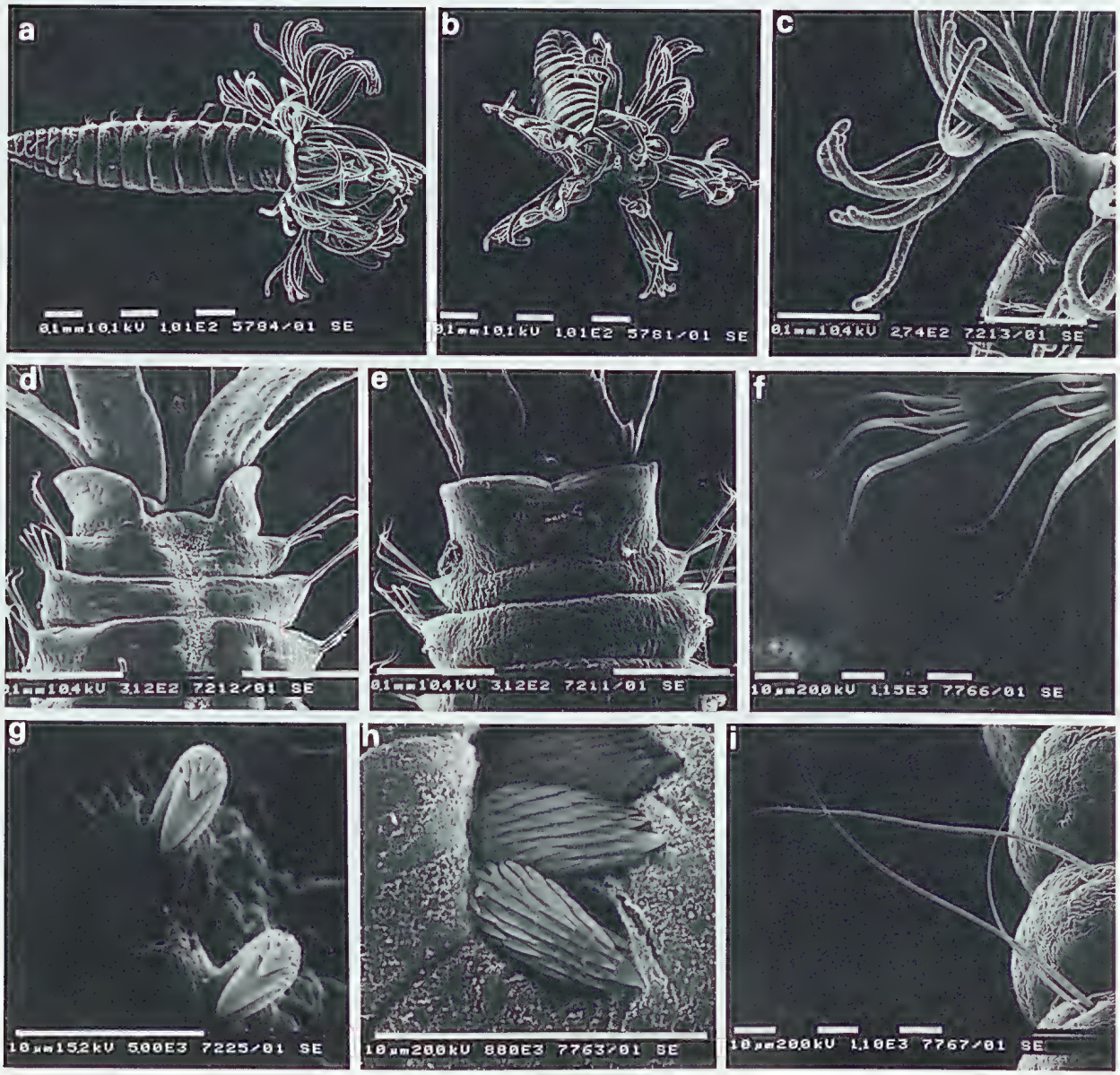


**Fig.5.** *Oriopsis mobilis* n.sp. (AM W 203559): a. S.E.M. oblique ventral view of whole animal. b. S.E.M. frontal view of crown showing three pairs of radioles. c. S.E.M. view of one radiole showing lateral flanges characteristic of *Oriopsis*. d. S.E.M. dorsal view of collar region. e. S.E.M. view of collar region showing ventral notch. f. S.E.M. showing long and short limbate capillary notosetae of thorax. g. S.E.M. showing thoracic uncini. h. S.E.M. showing abdominal uncini. i. S.E.M. showing capillary neurosetae of abdomen. Scale indicated by white bar and bottom left measurement on each figure.

Hartmann-Schröder, 1986: 60–61.

**Type species.** *Augeneriella hummelincki* Banse, 1957, by original designation.

**Diagnosis.** Fabricinae with 2 or 3 pairs of radioles each with 4–10 pairs of pinnules. Radioles free to base with no webbing, flanges or eyes. Branchial hearts present, one at base of each half of tentacular crown. Ventrally, between halves of tentacular crown, 2 branched or unbranched vascularised respiratory filaments. Collar reduced dorsally and forms a lobe ventrally. 8 thoracic and 3 or 4 abdominal setigers. Thoracic notosetae, spatulate and/or limbate capillaries. Thoracic neurosetae, on setigers 2–8 only, acicular uncini with several rows of teeth above the basal tooth. Abdominal notosetae uncini with long handles. Abdominal neurosetae straight capillaries.

**Comments.** The generic diagnosis has been emended as currently defined to include species with two pairs of radioles, unbranched ventral filaments and/or four abdominal setigers.

Hartmann-Schröder (1965) expressed reservations when including *Augeneriella dubia* in this genus due to its unbranched ventral filaments and the abdomen having four setigers instead of three. Gitay (1970) suggested that the definition of *Augeneriella* be emended to only include species of the Fabricinae with branched ventral filaments. However Hartmann-Schröder, when describing *Augeneriella bansei* Hartmann-Schröder, 1986 argued, but did not formally change the definition, that *A. bansei* showed similarities to *A. dubia* in having unbranched ventral vascularised filaments, and to the remaining species in the genus on the basis of setal structure, abdominal segmentation and collar structure. On this basis she felt *A. bansei* was a link between *A. dubia* and the remaining species of *Augeneriella* and both species should remain in the genus. This has been accepted in this study, however studies of reproduction in the Fabricinae (Rouse, in preparation) indicates detailed internal anatomical study is necessary to properly define *Augeneriella* and other fabriciin genera.

### *Augeneriella* cf. *dubia* Hartmann-Schröder

Fig.6a–k

*Augeneriella dubia* Hartmann-Schröder, 1965: 156–158, figs 84–85.—Gitay, 1970: 108.

**Material examined.** Queensland, Great Barrier Reef, One Tree Reef, 23°30'S 152°05'E. (AM W 20206, in 70% alcohol), 4 (AM W 203561, on S.E.M. stub). Queensland, Great Barrier Reef, One Tree Reef, 23°30'S 152°05'E. 30 specimens (AMNH). All collected 12 June 1987 by the author.

**Description.** Mature adults have 8 thoracic and 4 abdominal setigers (Fig.6a). A pair of semicircular branchial lobes arise from prostomium. Each lobe contains a branchial heart. 3 radioles arise from each branchial lobe, ending with a terminal pinnule similar in thickness to 6–7 pairs of pinnules extending from inner side of radioles (Fig.6a,b,c). 2 unbranched filaments, originating between ventral halves of radiolar crown, extend for half radiole length (Fig.6d). In live specimens these filaments alternately fill with green blood from branchial hearts. Semicircular lip from peristomium lies ventral to vascularised filaments (Fig.6c). Surface of lip completely ciliated and in females contains a pair of darkly pigmented spermathecae (Fig.6k). Collar reduced to a thickened ridge behind ventral lip (Fig.6b,c). No eyes or statocysts in preserved specimens, however in live material a pair of red eyes apparent in first segment and in pygidium. A pair of statocysts can also be found in first setiger when alive.

Notosetae of setiger 1 and following thoracic notopodia have 3–5 superior, long limbate setae and 3–5 inferior, short bilimbate setae (Fig.6e). Thoracic uncini have straight, long handles with large basal tooth and numerous rows of small teeth extending over crest (Fig.6f,g). There are 4–9 uncini per neuropodium. Abdominal notopodia have uncini with long handles and numerous rows of teeth (Fig.6j). Number of uncini per torus varies from 21 anteriorly to 13 on posterior setigers (Fig.6h). Abdominal neuropodia have simple capillaries with 3–4 long and 4–5 short setae per torus (Fig.6i).

Pygidium semicircular. Faecal groove runs ventrally along abdomen and dorsally along thorax. Lined, on all specimens, by numerous peritrich ciliates (Fig.6a,h). Preserved material opaque and dark brown anteriorly. Tubes fragile and closely fitting around occupant, composed of fine white coral sediment and mucous.

Females can be distinguished from males by their spermathecae located in ventral lip. Juveniles distinguished from adults in having only 3 abdominal setigers. Live material uniformly black with yellow patches at base of radiolar crown. Females have red eggs in last three thoracic setigers. In life branchial heart and filament systems expand and contract alternately pumping green blood.

**Comments.** The material from the Great Barrier Reef closely matches Hartmann-Schröder's original description. Therefore the distribution of *Augeneriella dubia* Hartmann-Schröder, 1965 has tentatively been extended from the type locality of Hawaii to Australia. The description of *A. dubia* differs only slightly from the Australian material in having fewer uncini in abdominal tori (up to 21 in Australian material compared to 26). The type material of *A. dubia* is restricted to the holotype and this is incomplete and in very poor condition (Fitzhugh, personal communication). Until new material is examined from the type locality the identification recorded here must remain uncertain.

*Augeneriella dubia* is distinguishable in the unbranched nature of the ventral filaments of the

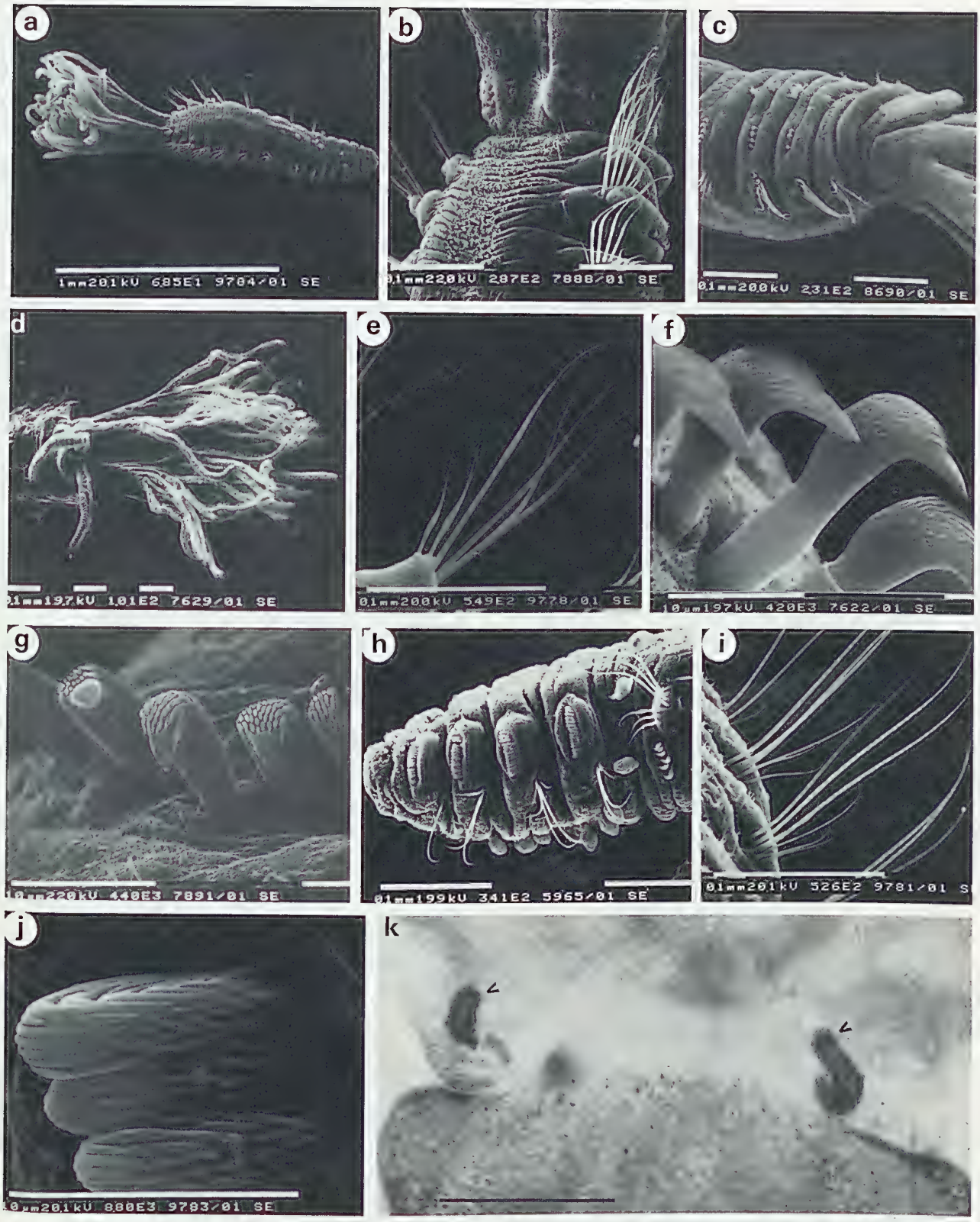


**Fig.6.** *Augeneriella* cf. *dubia* Hartmann-Schröder. Material from One Tree Reef, Great Barrier Reef, Australia. (AM W 203561): a. S.E.M. dorsal view of whole animal. b. S.E.M. dorsal view of anterior region showing reduction of collar. c. S.E.M. side view of collar region. Note ventral lip. d. S.E.M. ventral view of the crown showing the two unbranched blood vessels. e. S.E.M. showing long limbate and shorter bilimbate notosetae of thorax. f. S.E.M. showing side view of thoracic uncini. g. S.E.M. showing frontal view of thoracic uncini. h. S.E.M. showing abdominal region. Note peritrich ciliates on faecal groove. i. S.E.M. showing capillary neurosetae of abdomen. j. S.E.M. view of abdominal uncini. Scale indicated by white bar and bottom left measurement on each figure. k. Light micrograph of living female specimen showing the pair of darkly pigmented spermathecae (indicated by arrows) in the ventral lip. Scale bar is 150 µm.

crown, the lack of true spatulate notosetae in the thorax and the presence of four abdominal setigers instead of three. The observation of distinct spermathecae in the ventral lip of female specimens after preservation may prove to be an important generic feature. Rouse (in preparation) has observed spermathecae in several fabriciin genera. The spermathecae can be associated with the collar, crown or ventral lip. Examination of other species within *Augeneriella* for this feature may allow a better definition of the genus.

**Habitat.** Found intertidally in high densities (to 100,000 $m^2$) in mats of *Boodlia composita*, a green filamentous alga, on the upper reef crest on the north-eastern side of One Tree Reef.

**Distribution.** Hawaii, Australia (Great Barrier Reef, One Tree Reef).

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# *Dendrolagus scottae* n.sp. (Marsupialia: Macropodidae): a New Tree-kangaroo from Papua New Guinea

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ABSTRACT. *Dendrolagus scottae* n.sp. inhabits mossy forest above 1,200 m on the North Coast Range, Papua New Guinea. Its total known habitat area is estimated at about 25-40 km$^2$. The species is gravely endangered, and its plight is symptomatic of that of many large mammals in Melanesia. *Dendrolagus scottae* differs from all other tree-kangaroos in its uniform blackish colouration, narrow but long dentary, shallow face, and wide P/3 with a large posterobuccal cusp. The combination of large cheekteeth but small masticatory muscles suggest that *D. scottae* n.sp. has a different feeding strategy to other tree-kangaroos. *Dendrolagus scottae* n.sp. and *D. dorianus* possess a number of features which are unique among near relatives. These include the presence of a greatly reduced superior lachrymal foramen, large cheekteeth, uniformly dark dorsal and ventral colouration, and a very short tail. These derived features indicate that these two species are each other's closest relatives.

FLANNERY, T.F. & L. SERI, 1990. *Dendrolagus scottae* n.sp. (Marsupialia: Macropodidae): a new tree-kangaroo from Papua New Guinea. Records of the Australian Museum 42(3): 237–245.

The tree-kangaroos (genus *Dendrolagus*) are the only arboreal members of the marsupial family Macropodidae, which also includes the more familiar terrestrial kangaroos and wallabies. Tree-kangaroos are restricted to the rainforests of both north-eastern Australia (two species) and New Guinea (seven species). The two Australian species and the New Guinean *Dendrolagus inustus* form a plesiomorphic group (Groves, 1982; Flannery & Szalay, 1982). *Dendrolagus inustus* is the only species previously reported from the North Coast Range. A group of specialised, highly arboreally-adapted species inhabits the New Guinean Central Cordillera and some outlying ranges (Groves, 1982) (Fig.1). *Dendrolagus dorianus* is the most apomorphic member of this group. It is largely restricted to high-altitude mossy forests along the Central Cordillera, but one subspecies inhabits the Wondiwoi Peninsula of Irian Jaya. *Dendrolagus dorianus*, the largest previously-known species, is almost bear-like in its proportions, with fore- and hindlimbs subequal in length, a domed forehead and a very short tail. In addition to the living species, a very large extinct species (*Dendrolagus noibano*) is known from Pleistocene fossil remains from Chimbu Province Papua New Guinea (Flannery, Mountain & Aplin, 1983). It is dentally and

proportionally very similar to *D. dorianus* and *D. goodfellowi*, and differs from *D. scottae* n.sp. in its robust dentary and relatively narrow P/3.

## Materials and Methods

Specimens of *Dendrolagus scottae* n.sp. were compared with the tree-kangaroo specimens held in the Australian and Macleay Museums, Sydney; and the Australian National Wildlife Collection, Canberra. All known species of *Dendrolagus*, as well as the holotypes or lectotypes of *D. dorianus*, *D. spadix* and *D. deltae* are held in these collections. In addition, one of the paralectotypes of *D. ursinus* was borrowed from the Rijksmuseum van Natuurlijke Historie, Leyden, and the holotype of *D. d. mayri* was examined during a visit to the British Museum of Natural History. Examination of the excellent colour plates, skull photographs and descriptions of Rothschild & Dollman (1936) provided data for the types that could not be examined personally. Colours where capitalised follow Smythe (1974). Museum acronyms are: AMM = Australian Museum mammal specimen; CM = National Wildlife Collection Mammal specimen. All measurements in millimetres and weights are in grams. The Appendix contains the Table referred to in this paper.

## Systematics

**Macropodidae** Gray, 1821

***Dendrolagus*** Müller, 1840

***Dendrolagus scottae* n.sp.**

Figs 2–4, Table 1

**Type material.** HOLOTYPE: AMM19481, study skin and skull of a juvenile collected 11 June 1988 at about 1,400 m on Sweipini (3°23'S 142°06'E), a ridge just to the west of the Mount Somoro summit, Torricelli Mountains, West Sepik Province, Papua New Guinea. PARATYPES: AMM19491, adult partial skull and dentaries kept as

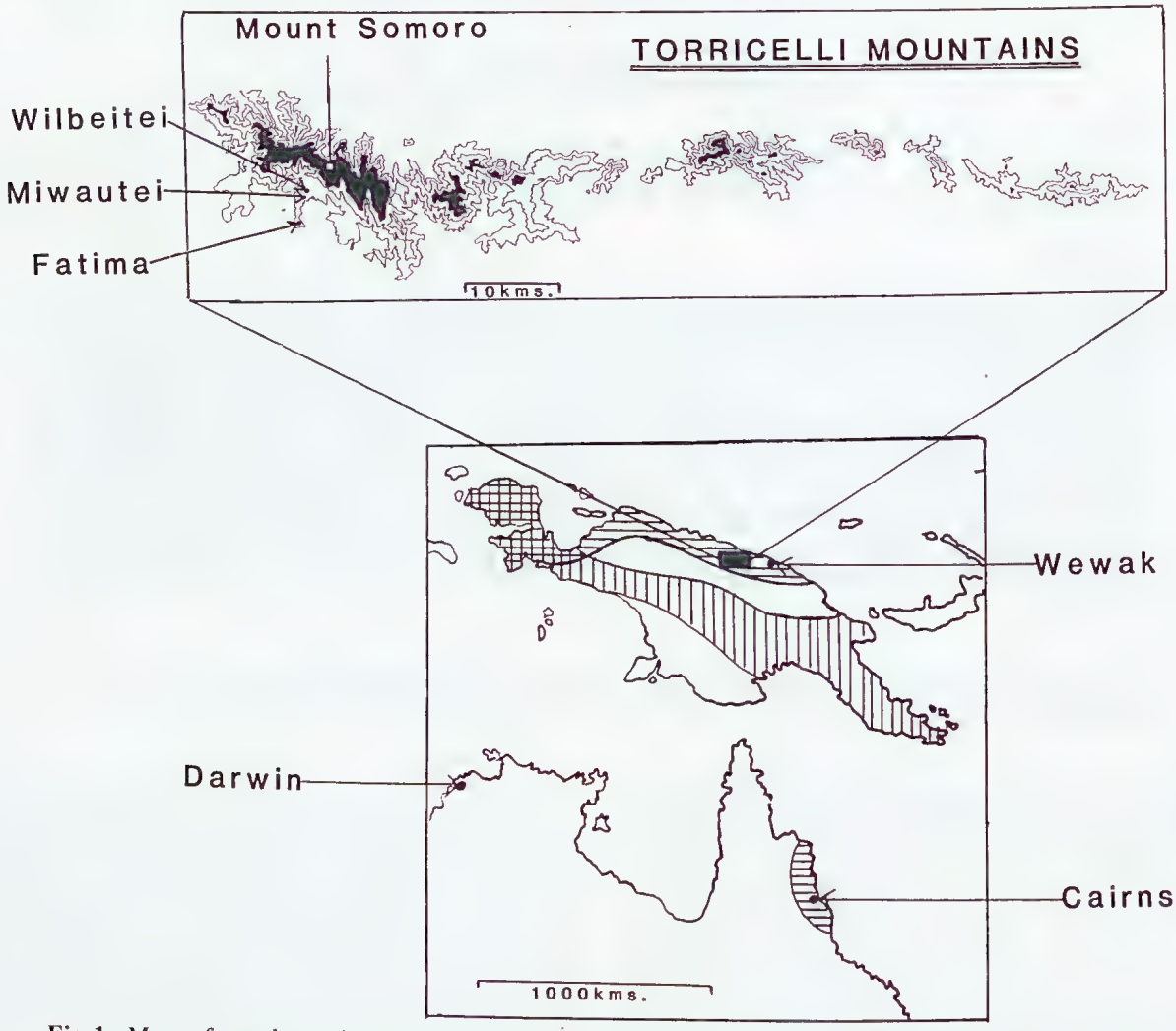


**Fig.1.** Map of northern Australia and New Guinea, showing the distribution of tree-kangaroos. Horizontal bars = plesiomorphic species group; vertical bars = derived species group (see text for explanation). Inset: The Torricelli Mountains (showing 800 m and 1,000 m contours), with shaded area being land above 1,200 m, and localities mentioned in the text.

trophies by Olo hunters, and purchased on 21 July 1985 at Wigote Village (3°27'S 142°10'E), Torricelli Mountains. They are taken to represent a single individual as they were bought together and the size and patterns of dental wear match. AMM20948, segment of dorsal fur of adult, extending from neck to base of tail, sex unknown. Collected by Olo hunter in Mount Somoro area in April 1989 and given to Fr P. MacGeaver for transmission to the Australian Museum, Sydney.

**Other specimens.** 14 fragmentary dentaries, including 1 juvenile, purchased at Wigote Village, Torricelli Mountains, on 21 July 1985 and 11 March 1990.

**Diagnosis.** *Dendrolagus scottae* n.sp. differs from all other species of tree-kangaroo in its overall blackish colouration (Fig.2), its small masticatory muscle mass relative to cheektooth size, shallow face (Fig.4), and consistent development of a large posterobuccal cusp on P/3 (Fig.4). It further differs from all other species of *Dendrolagus* except *D. dorianus* in its large size, extremely short tail, minute superior lachrymal foramen and large cheekteeth. It further differs from *D. dorianus* in that the lower incisors are less procumbent, and P/3 is broader (Figs 4,6), and in that the hair whorl is placed further anteriorly (Fig.2). It further differs from *D. ursinus* in lacking a white throat, tufted ears, and in having the venter dark, not contrasting with the dorsum.

**Description.** The following description is based upon the juvenile holotype, with supplementary references to the fragmentary paratypes where appropriate. Comparisons with *D. dorianus* are given. The dorsum and venter are uniform, and close to Sepia. On the paratype adult skin fragment (which represents most of the back and is 740 mm long and 230 mm wide in the middle) the overall colour is close to Jet Black, being slightly more intensely black than that area of the juvenile. The hair bases are brown, the black effect coming from the black hair tips and long black guard hairs. The fur, particularly on the neck, is coarser in texture than on the juvenile. *Dendrolagus dorianus* differs in that the dorsum is either golden (as in the only known specimen of *D. d. mayri*) or some shade of brown. The darkest specimens are some *D. d. notatus*, where the tail is usually paler than the dorsum or has a generous scattering of pale hairs on a brown background.

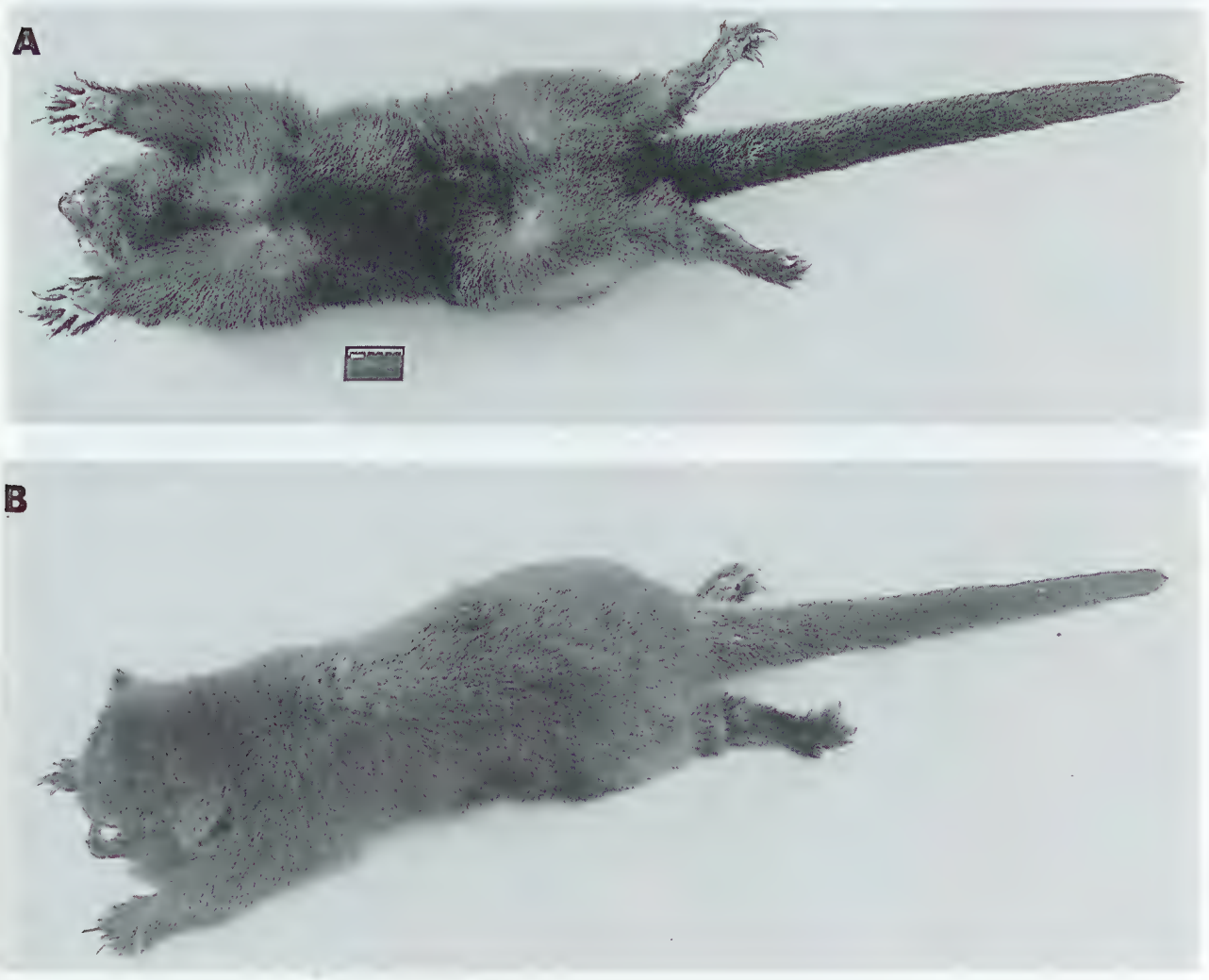


**Fig.2.** A, ventral and B, dorsal view of the holotype skin of *D. scottae* n.sp. (AMM19481).

On the holotype of *D. scottae* a sharp line, running from ear to ear, divides the Dark Drab face from the Sepia dorsum. Most of the tail, the dorsal surfaces of the hands and feet, and the ears, are Jet Black. By contrast the limbs and tail are paler in *D. dorianus*. A few silvery hairs encircle the tail base, and a small cluster of Yellow Ocher hairs is present anterior to the silver hairs on the dorsal side of the tail base. On the paratype adult skin fragment the patch of light hair at the tail base is relatively large (45 mm *x* 23 mm), and is pale yellow grading to Yellow Ocher at its centre. On the holotype the dorsal surface of the lower leg is Dark Drab. A distinct hair whorl is positioned in the middle of the back just behind the shoulders. On the paratype the hair whorl is placed well anteriorly (although unfortunately without the limbs it is difficult to say precisely where).

Except for the features noted in the diagnosis, the skull of the juvenile holotype is largely similar in overall shape to that of a similar-aged *D. dorianus*. However, it differs in that the interparietal is broader and anteroposteriorly shorter, and in that the nasals are narrower. Unfortunately, our limited sample of juvenile *D. dorianus* is insufficient to establish whether these are consistent differences between the species.

It is difficult to estimate the adult body weight of *Dendrolagus scottae* n.sp. The species is probably sexually dimorphic in size, as are the other large tree-kangaroos. The only specimen for which we have body weight is a female pouch young. It has only M2 erupted, and weighed 1,500 g. By comparison a male *D. dorianus* (AMM19436) that weighed 1,300 g already has M3 erupted. Two of the three complete adult dentaries of *D. scottae* n.sp. are longer than a wild caught male *D. dorianus* (CM12303) that weighed 20,000 g (the largest weight ever recorded for a tree-kangaroo).

The fragmentary adult crania and dentaries of *D. scottae* n.sp. differ from those of *D. dorianus* in the following ways. The dentary is larger overall, but much more gracile (Fig.4). The inflection of the angle and attachment points for the pterygoid musculature are greatly reduced; so much so that when viewed laterally, the inflected angle does not project posteriorly any further than the condyle (Fig.4). In all *D. dorianus* examined the projection of the inflected angle beyond the condyle is marked. In addition, the ridge below the masseteric foramen that serves for the point of attachment for the superficial layer of the masseters is very small relative to *D. dorianus*. The body

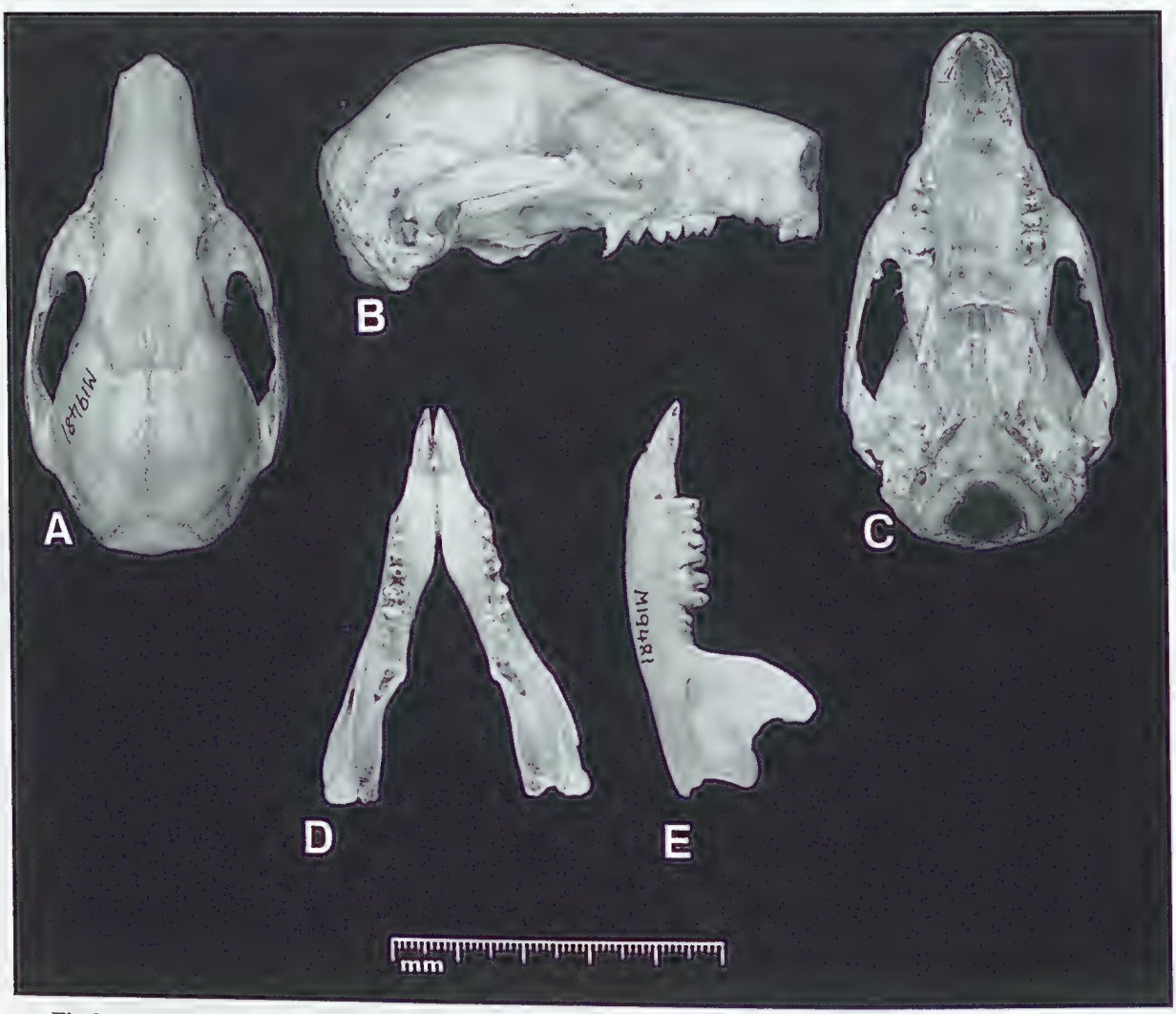


**Fig.3.** Cranium and dentaries of the holotype of *D. scottae* n.sp. (AMM19481) in A, dorsal, B, lateral, C, ventral, D, occlusal and E, lingual views.

of the dentary itself is more gracile although the teeth are large, and the dentary relatively long (Fig.5). The adult masseteric arch in *D. scottae* n.sp. also differs greatly from that of *D. dorianus*. It is shallow anteriorly in *D. scottae*, with only a trace of a zygomatic process present on the adult paratype (although a modestly developed process is present in the juvenile). Posteriorly, the zygomatic arch is deep, while the postglenoid process is relatively small. The zygomatic arch is relatively longer than in*D. dorianus*, but the points of attachment for the masseters are relatively very small.

**Etymology.** Named for the late Winifred Violet Scott, an endowment from whose estate has enabled a programme of research and conservation of this species.

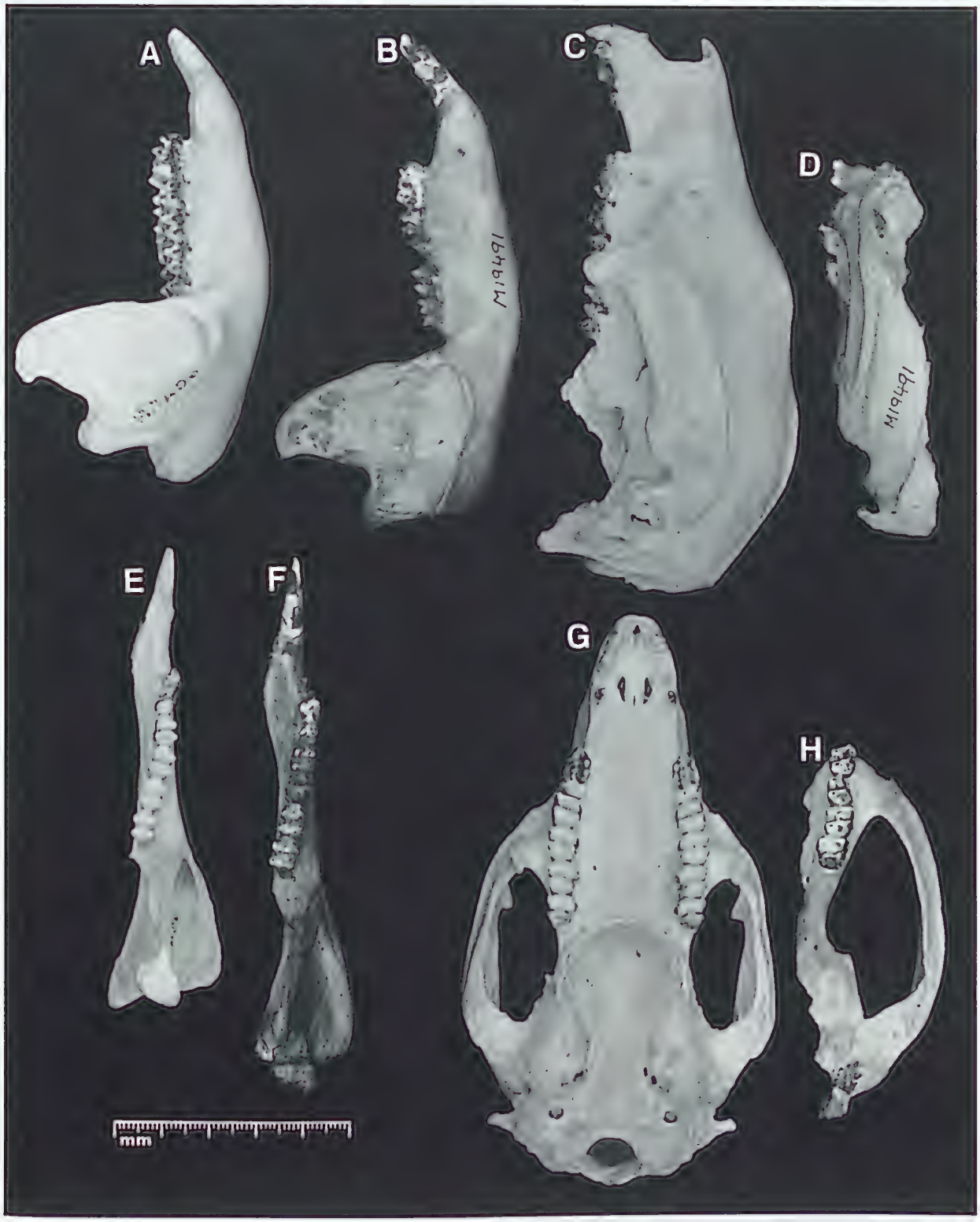


**Fig.4.** Paratype of *D. scottae* n.sp (AMM19491) (B,D,F,H), compared with *D. dorianus* (AMM7406) (A,C,E,G), adult female, Mount Hagen district.

## Discussion

**Relationships.** *Dendrolagus scottae* n.sp. possesses internally furred ears, a distinctively short, broad foot, and a relatively very shortened fourth toe. These are synapomorphic features which Groves (1982) notes are also present in *D. dorianus*, *D. matschiei* and *D. ursinus*. These features are convincing evidence that these four species form a clade within *Dendrolagus*. Within this clade, *Dendrolagus scottae* n.sp. shares a further suite of derived features with *D. dorianus* which suggest that these species may be sister taxa. These include a reduction in the size of the superior lachrymal foramen

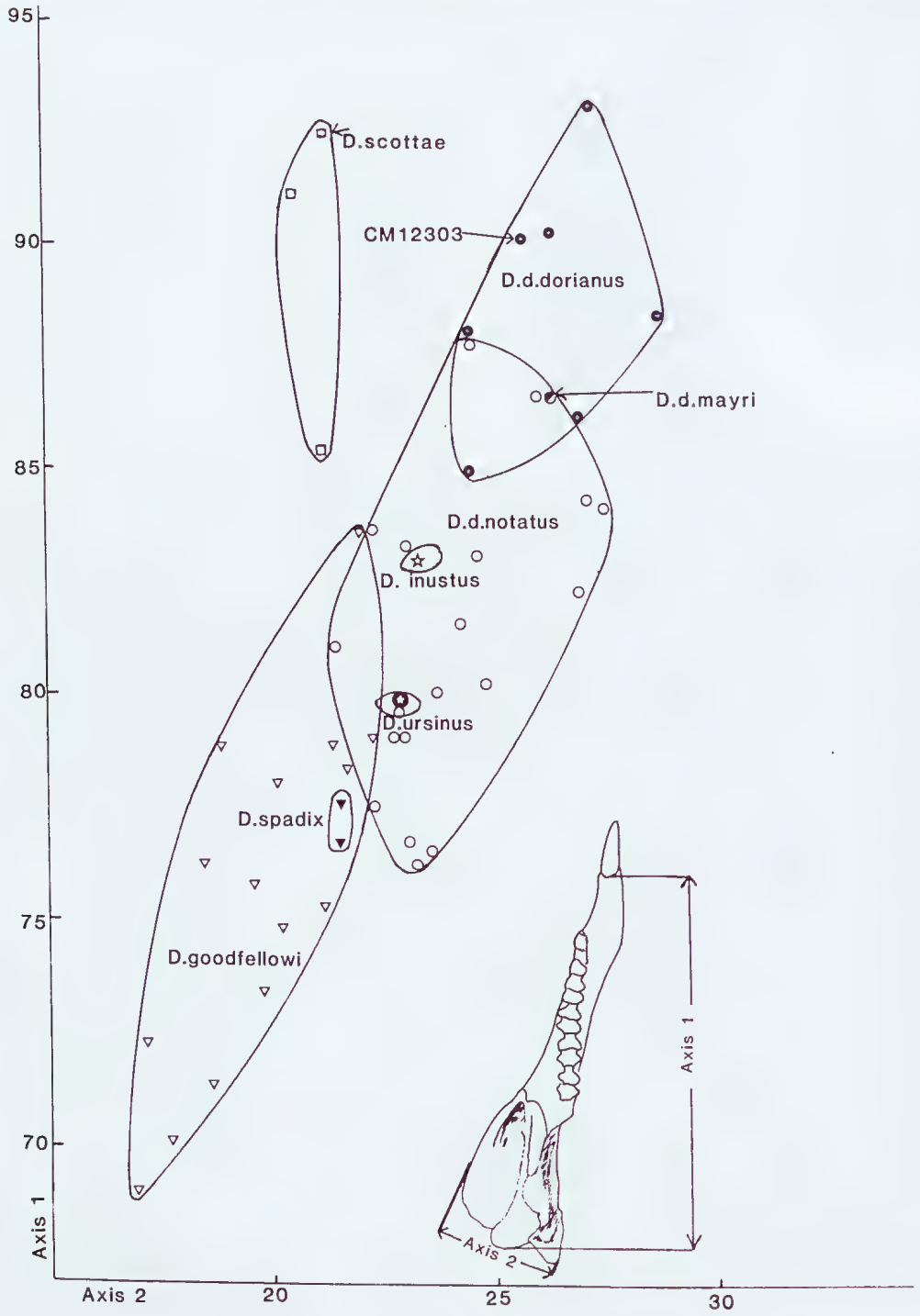


**Fig.5.** Bivariate plot of dentary length (from condyle to I/1 alveolus, vertical axis) over maximum width of the posterior of the dentary (horizontal axis) for *Dendrolagus dorianus dorianus* (dots), *D. d. notatus* (circles), *D. d. mayri* (half filled circle), and *D. scottae* n.sp. (squares), *D. goodfellowi* (inverted hollow triangles), *D. spadix* (inverted solid triangles), *D. inustus* (star), *D. ursinus* (enclosed star).

(unique within *Dendrolagus*, Groves, 1982), large cheekteeth (Groves, 1982; Fig.4), a very short tail (which contrary to Groves, 1982 is relatively longer in *D. ursinus* than *D. dorianus*), and a dark (brown or blackish) ventral and dorsal colouration. This suite of features is persuasive evidence that *D. dorianus* and *D. scottae* n.sp. are each other's nearest relatives.

*Dendrolagus dorianus* and *D. scottae* n.sp. differ however in a number of ways. *Dendrolagus dorianus* possesses a hairwhorl which is placed near the base of the tail. In *D. scottae* n.sp. the hairwhorl is situated just posterior to the shoulders (which is the plesiomorphic condition, Groves, 1982). In *D. ursinus* it is positioned as in *D. scottae* n.sp., while in *D. matschiei* it is placed further posteriorly. Furthermore, the dentition and masticatory apparatus of *D. scottae* n.sp. and *D. dorianus* differ greatly. The P/3 of *D. scottae* n.sp. is relatively broader than in *D. dorianus* (Fig.6). In addition, the dentary is very large, yet more gracile, with the points of insertion for the masseters, temporals and pterygoids much reduced (Fig.5). These features are consistent with a species, rather than subspecies level difference (they are not seen, for example, between the subspecies of *D. dorianus*), and they seem to indicate a major difference in diet between *D. scottae* n.sp. and all other species of *Dendrolagus* examined.

**Distribution and conservation status.** *Dendrolagus scottae* n.sp. has one of the smallest distributions of any Melanesian mammal. Thus far it is known only from the Torricelli Mountains of West Sepik Province, Papua New Guinea. Olo speaking hunters from the Mount Somoro area indicate that the species is restricted to the mossy forest near the summit of the Torricelli Mountains. Mossy forest is well developed only above 1,400 m, but we have mapped the potential range

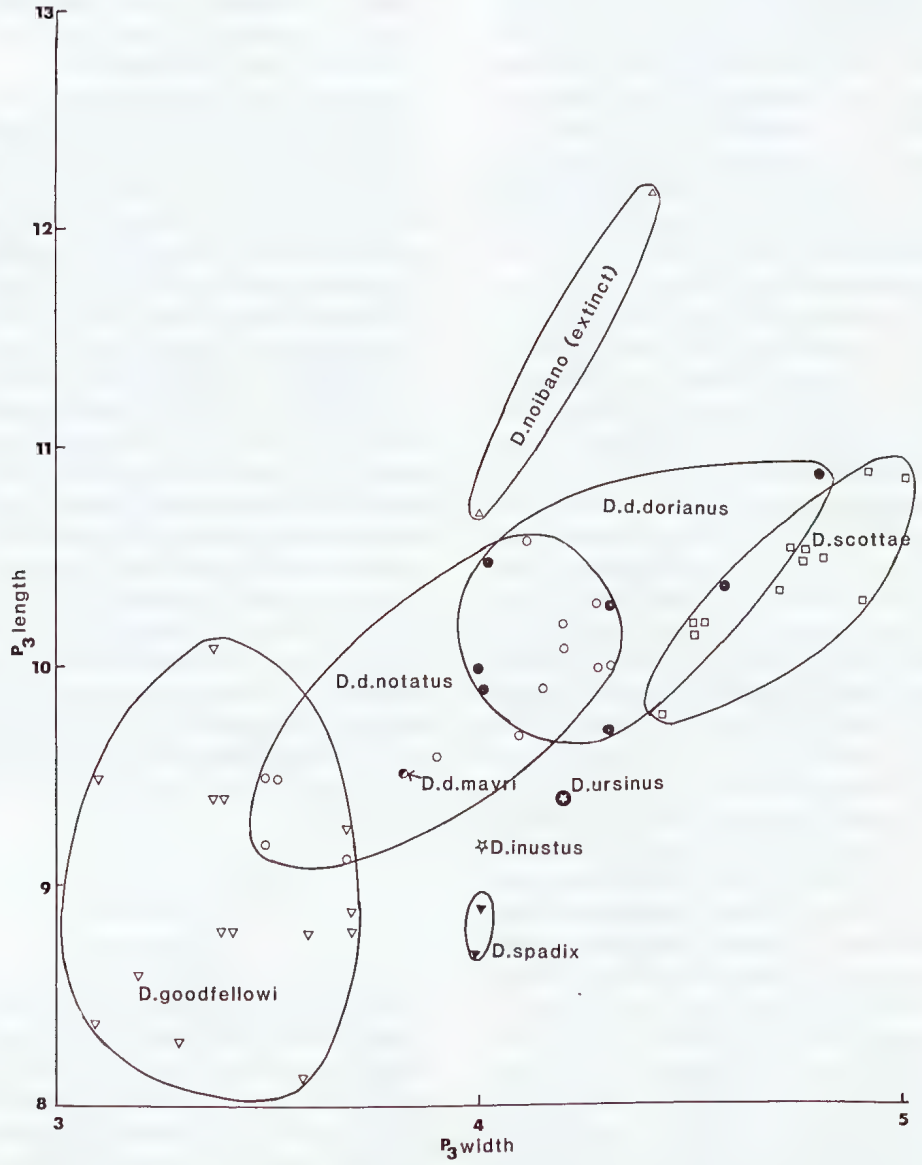


**Fig.6.** Bivariate plot of P/3 length (vertical axis) over P/3 maximum breadth (horizontal axis) for the New Guinean species of *Dendrolagus*. Symbols as in Figure 5 with the addition that *D. noibano* = triangles.

of *D. scottae* n.sp. as coinciding with the 1,200 m contour, as local topography may allow the species to utilise some of this lower forest (Fig.1). Indeed, experienced Olo tree-kangaroo hunters agreed that *D. scottae* n.sp. spends the wet season on the mountain ridges, and during the dry season shelters in deep gullies on the summit flanks, to avoid the heat. Even given this more generous potential distribution, its potential habitat estimated by this method covers only 39 km$^2$. This is, however, fragmented. The largest fragment, which includes Mount Somoro, covers 24 km$^2$. The next largest fragment is only 6.8 km$^2$ in extent and lies 4.7 km to the east, being separated by country as low as 640 m. Two uninvestigated mountain ranges lie to the west of the Torricelli Mountains, and may provide habitat for *D. scottae* n.sp. An unnamed range 31 km to the west, and separated by saddles as low as 640 m, has some 40 km$^2$ above 1,200 m. Again, however, it is divided into many fragments, the largest being only 27 km$^2$. The Bewani Mountains lie 37 km to the west of the unnamed range, and are separated from it by country as low as 500 m. Approximately 45 km$^2$ of habitat above 1,200 m is present there, and it forms a single large block. It is possible that during Pleistocene glacial maxima, depressed vegetational zonation due to lowered temperatures may have allowed contact between the mossy forests of all of these now separated blocks. If this is so, and no local extinction has taken place, they may well currently provide habitat for *D. scottae* n.sp. We can locate no other potential areas of suitable habitat.

Olo informants considered that three distinct kinds of tree-kangaroos originally inhabited the Torricelli Mountains. The local names for these are Tenkile (= *D. scottae* n.sp.), Yonki (= *D. inustus*) and Weimanke. According to all informants questioned, Weimanke is now extinct in the Torricelli Mountains.

One old man (who appeared to be in his 70's) said that his father had captured a Weimanke in the Mount Somoro area when the informant was a child. Several older men had seen skins of the species retained as "Bilas" (decoration), and all said that its fur was brown, the tail long and mottled, and the facial skin was pink, or as they said, like the face of Europeans. One man who had travelled to Lae said that he had seen the species in a market; the animal he described was almost certainly *D. goodfellowi*. Thus Weimanke may have been *D. goodfellowi* or a related species.

The very small known distribution of such a large animal as *D. scottae* n.sp. is surely indicative of a small population size. There are no studies of tree-kangaroo population densities, so it is difficult at present to estimate the overall population size. However, an estimate based upon densities of other, similar-sized rainforest-dwelling mammals (e.g. *Hyemoschus aquaticus*, see Nowak & Paradiso, 1983) suggests that the total population of *D. scottae* n.sp. in the Torricelli Mountains is in the low hundreds. These data, along with observations of recent human activity in the Torricelli Mountains, suggests that *D. scottae* n.sp. is imperilled. The extinction of *D. goodfellowi* or a near relative in the Torricelli Mountains, almost certainly through human predation in the last 60 years, bodes ill for *D. scottae* n.sp. Human utilisation of the region is increasing. Moderately high (and growing) human population densities occur throughout the lower and middle slopes of the Torricellis (King & Ranck, 1980), although there is no permanent human settlement in the moss forest zone itself. A road now links Wilbeite Village (altitude 920 m) with the major regional centre of Lumi, and a well-defined foot track crosses the Mount Somoro montane block from Wilbeite to Aitape. The summit of Mount Somoro has been cleared, and a semi-permanent camp erected for workers who will construct a telecommunications repeater station there. Increased human activity in this area already seems to have led to the extirpation of *D. scottae* n.sp. in the middle of its distribution, for we could find no evidence of it persisting there during our 1988 fieldwork. The increased availability of shotguns over the past few decades has doubtless adversely affected the species. Other large Melanesian mammals have similarly been adversely affected by growing human populations and changing technologies (George, 1978).

Recent studies have shown that the mossy forests of the North Coast Range shelter an unusual mammal assemblage. The large, recently described gliding possum *Petaurus abidi* Ziegler, 1981, and the hydromyine murid *Paraleptomys rufilatus* Osgood, 1945 are endemic to the North Coast Range; while a second endemic hydromyine from the Mount Somoro area has recently been recognised by one of us (Flannery, in press). A further striking feature of the mammalian fauna of the mossy forests of the North Coast Range is the absence of otherwise widespread groups. Our 1985 and 1988 fieldwork has confirmed that species of *Rattus* and *Phalanger* (*sensu stricto* e.g. Flannery, Archer & Maynes, 1987) are absent from this habitat. Elsewhere in montane New Guinea these are usually the most species rich genera of the terrestrial and arboreal mammal assemblages respectively, with up to four congeners existing in sympatry (Flannery, 1987; Taylor *et al.*, 1982). These differences in the mammal fauna of the mossy forests of the North Coast Range and the rest of montane New Guinea suggests that the North Coast Range has been long isolated from the Central Cordillera, and that its mammalian assemblage is unique. *Dendrolagus scottae* n.sp. is clearly a part of this unique fauna.

## Summary

*Dendrolagus scottae* n.sp. is restricted to mossy forests on part of the North Coast Range, Papua New Guinea. Its nearest relative is *D. dorianus* of the Central Cordillera, from which it differs in masticatory adaptations, size, colour and morphology. It is endangered, primarily due to high levels of human predation and disturbance over all of its small range.

ACKNOWLEDGMENTS. At the time this paper had gone to press funding for a comprehensive research and conservation programme for *Dendrolagus scottae* n.sp. had been obtained from the estate of the late Winifred Violet Scott. We wish to acknowledge here the generosity of the trustees of the estate in supporting further studies of this endangered species. We wish also to thank Karol Kisokau OBE, Secretary of the P.N.G. Department of Environment and Conservation, and his staff, for their help with this project; for without them this discovery would never have been made. We also wish to thank the Australian Museum Trust for a grant that allowed this fieldwork to be carried out, and Fr Patrick McGeaver and Sr Cecilia Prest of Fatima Catholic Mission for their help in the field. Also, Francis Ulel, Magistrate of Wilbeite Village, is thanked for his help. Ms T. Ennis accompanied us on the 1988 expedition, and drafted the figures for this work. We are grateful to Drs J. Calaby, A. Greer and Mr S. Van Dyck for critically reading this manuscript.

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## APPENDIX

Table 1. Some measurements for the holotype of *D. scottae* n.sp. and some measurements of the dentary of adults of *D. scottae* n.sp. (all trophy dentaries; including AMM19491: paratype). X = mean, R = range, S = standard deviation, N = sample size).

*D. scottae* n.sp. AMM19481 (holotype)

Head-body length = 322
Tail-vent length = 280
Hindfoot length (s.u.) =72.8
Ear length (notch) = 44
Weight = 1,500

condylobasal length = 73.9
bizygomatic width = 42.7
P2/-M1/ length = 10.1
M1/ width = 4.8
posterior nasal width = 13.3
Nasal length = 28.2
interorbital breadth = 14.6
maximum length = 78.5

| | P/3-M/5 length | P/3 length | P/3 width | M/4 width | diastema length | dentary depth below M/2 |
|---|---|---|---|---|---|---|
| X | 37.5 | 10.4 | 4.7 | 5.7 | 12.3 | 17.5 |
| R | 36.1-38.7 | 9.8-10.9 | 4.3-5.0 | 5.4-5.9 | 10.6-13.5 | 15.2-19.0 |
| S | .83 | .37 | .25 | .14 | .91 | 1.17 |
| N | 8 | 8 | 9 | 9 | 10 | 10 |

Records of the Australian Museum (1990) Vol. 42: 247–300. ISSN 0067–1975



# The Genera *Catoessa*, *Elthusa*, *Enispa*, *Ichthyoxenus*, *Idusa*, *Livoneca* and *Norileca* n.gen. (Isopoda, Cymothoidae), Crustacean Parasites of Marine Fishes, with Descriptions of Eastern Australian Species

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ABSTRACT. The following genera of Cymothoidae are recorded from Australia: *Catoessa* Schiödte & Meinert, *Elthusa* Schiödte & Meinert, *Enispa* Schiödte & Meinert, *Ichthyoxenus* Herklots, *Livoneca* Leach and *Norileca* n.gen. Full diagnoses are given for *Enispa*, *Livoneca* and *Norileca* n.gen. For the remaining genera provisional diagnoses are given. *Idusa* Schiödte & Meinert is rediagnosed to allow separation from *Catoessa*. All the species described herein would have previously been placed in *Livoneca*. Examination of the type material of *L. redmanii* shows that all other species placed in the genus, except for *L. bowmani* Brusca, are not congeners, and are reassigned, where possible, to other genera. The genus *Livoneca* is found to belong to the Anilocrinae, and is most closely related to the *Nerocila* group of genera. The principal characters used in redefining these genera and assigning *Livoneca* and *Norileca* to the Anilocrinae are the morphology of the brood pouch, pleopods, pleon and cephalon. The species described are *Catoessa ambassae* n.sp., *Elthusa myripristae* n.sp., *E. neocytta* (Avdeev), *E. propinqua* (Richardson), *E. raynaudii* (Milne-Edwards), *E. sacciger* (Richardson), *E. sigani* n.sp., *E. turgidula* (Hale), *Enispa irreqularis* (Bleeker), *Ichthyoxenus minabensis* (Shiino), *Norileca indica* (Milne-Edwards) and *Norileca triangulata* (Richardson). Discussion is given of the genera treated and the problems present in attempting to diagnose subfamilies within the Cymothoidae. Keys are given to the Australian gill attaching genera and the Australian species of the genera *Elthusa* and *Norileca*.

BRUCE, N.L., 1990. The genera *Catoessa*, *Elthusa*, *Enispa*, *Ichthyoxenus*, *Idusa*, *Livoneca* and *Norileca* n.gen., (Isopoda, Cymothoidae), crustacean parasites of marine fishes, with descriptions of eastern Australian species. Records of the Australian Museum 42(3): 247–300.

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This work was initially intended as an account of the species of *Livoneca* Leach, 1818, from Australia. As description of the species progressed it was increasingly apparent that the species under study could not be contained in a single genus. Bruce (1986) gave a diagnosis and description to *Mothocya* and attempted to tabulate comparable characters of *Livoneca*, also commenting that there were inconsistencies in morphology between the species currently being placed in *Livoneca*.

The distinction between *Livoneca* and genera such as *Elthusa*, *Idusa*, *Ichthyoxenus* and *Catoessa* has never been clear. Most species of *Idusa* have been incorrectly placed in that genus (Trilles, 1981). *Ichthyoxenus* and *Livoneca* have been considered synonymous by many authors (e.g. Fryer, 1965, 1968; Lincoln, 1972).

One of the main causes of confusion is that the type species of most of the genera concerned have not been fully described. *Livoneca redmanii*, type species of the genus, was figured by Schiödte & Meinert (1884), but remained effectively undescribed by modern standards. The type specimens have never been figured.A similar situation exists for most genera created by Schiödte & Meinert (1883, 1884).

In redescribing *L. redmanii* two major problems arose. Firstly the cephalic, pleonal, brood pouch and pleopod morphology indicate clearly that the species (and therefore the genus) is most closely allied to *Nerocila*. Secondly, none of the more than 70 species, other than *Livoneca bowmani* Brusca, 1981, subsequently placed in the genus appeared to belong to *Livoneca*. This created the problem of where to assign these most inadequately described species, since most genera of "Livonecinae" are effectively undiagnosed.

Other problems involved the status of the genera *Idusa* and *Ichthyoxenus* and their species. These are discussed in the respective generic sections.

To attempt at least a partial solution I have provided provisional diagnoses to those genera whose type species have not been fully described (*Catoessa*, *Elthusa*, *Ichthyoxenus* and *Idusa*), and where the type species is fully described (*Livoneca*, *Enispa*, *Norileca* n.gen.) I provide a full diagnosis and description.

Species have been assigned to genera on the basis of available descriptions or examination of the types. In many cases species are inadequately described, or types too fragile for detailed examination, and many species

have been placed where they fit best. Most species formerly in *Livoneca* are now placed in *Elthusa*.

As there has been so much confusion over correct generic placement of *Livoneca* species, I have provided a complete list of all species that have been placed in the genus in the past. The most recent comprehensive account is referred to for each species.

Prior to the present work there were few records of gill parasitic isopods from Australia. Hale (1926) recorded four species in two genera, and Avdeev (1975a,b, 1978) increased the total to three genera and seven species. Bruce (1986) added a further seven species, all *Mothocya*, to those known from Australia. The present work records another two genera and nine species (*Catoessa* and *Enispa* are buccal parasites, and the attachment site for *Ichthyoxenus minabensis* is unknown). A key is provided to the gill attaching genera known from Australia, together with keys to the Australian species treated here.

## Methods

Methods follow Bruce (1987a). No specimens were obtained by personal collecting, though several were obtained from fishes in the Australian Museum fish collections. In this instance the host fish catalogue number is also given. All fish identifications and names were confirmed by the Australian Museum fish section except where otherwise indicated. All isopod length measurements are in millimetres (mm).

Abbreviations used in the text are: AM – Australian Museum, Sydney, NSW, Australia; BMNH – British Museum (Natural History), London; MHNG – Muséum d'Histoire Naturelle, Geneva, Switzerland; NSW – New South Wales, Australia; NT – Northern Territory, Australia; NTM – Northern Territory Museum, Darwin, NT; Qld – Queensland, Australia; QM – Queensland Museum, Brisbane, Qld; RMNH – Riksmuseum van Natuurlijkie Historie, Leiden; SA – South Australia; SAM – South Australian Museum, Adelaide; Tas – Tasmania, Australia; USNM – Smithsonian Institution, Washington, D.C., USA; Vic – Victoria, Australia; WA – Western Australia; WAM – Western Australian Museum, Perth, WA; ZMA – Zoologisch Museum, Amsterdam.

## Host Preferences

For most of the species treated in this work there is insufficient data for any patterns of host use to emerge. The two species of *Norileca* are both associated with open water or pelagic schooling fishes. The genera *Catoessa*, *Enispa* and *Ichthyoxenus* are represented in Australia by a single species each. *Elthusa* is represented by seven species, but there is no discernible pattern. *Elthusa turgidula* is known only from tropical Scaridae, the temperate *E. neocytta* is recorded only from Zeidae and *E. propinqua* is recorded principally from Macrouridae. *Elthusa raynaudii* is in contrast recorded from a wide variety of hosts: eight species in seven genera and five families, plus unidentified hosts in a further two families. The remaining species either lack host data (*E. sacciger*) or are known from single records *E. myripristae*, *E. sigani*).

Position of attachment of these gill parasites varies considerably. *Elthusa myripristae* attaches in a ventral position on the gill, head anteriorly, abdomen against the host's body rather than gill operculum. *Elthusa turgidula* attaches in a medial position on the gill arches, with the head projecting into the buccal cavity. For the other species of *Elthusa* only 'gills' or 'gill cover' has been recorded.

*Norileca indica* has the head to the anterior, and the abdomen facing outwards, pressed against the gill operculum, positioned ventrally in the gill cavity. This is a position similar to that figured by Tiwari (1953) for *Agarna malayi*.

## Cymothoid Classification

Schiödte & Meinert (1881–1884) divided the Cymothoidae into several subfamilies. There were no further developments on cymothoid classification until Brusca (1981) gave his ideas on phylogeny and evolution within the family. Brusca's (1981) interpretation was similar to that offered by Schiödte & Meinert, but the discussion and rationale were far more detailed. Bruce (1987c) gave a diagnosis for the externally attaching lineage, the subfamily Anilocrinae. The principal characters involved in diagnosing the Anilocrinae were the morphology of the brood pouch, pleon and pleopods. No attempt was made to redefine other subfamilies as lack of data on the larger genera precluded assessment of their systematic position.

Recent work on cymothoid taxonomy has yielded many new descriptive and host data (studies by Williams & Williams 1980, 1981, 1986, 1987; Bruce, 1986, 1987a,b,c; Bruce & Bowman, 1989; and Bowman & Tareen, 1983). Host specificity has been shown to be far more restricted in several genera (e.g. *Anilocra*, *Renocila*, *Mothocya*) than previously supposed, while in others (*Nerocila*, temperate species of *Anilocra* and *Elthusa*) host specificity is weak. More importantly, the morphological characters now being described can shed new light on classification within the family.

Position on the host (buccal, gill, burrowing or external), and general body shape have long influenced interpretation of the relationships of cymothoid genera. In earlier classifications appendages were not considered, or at most were regarded as useful in species discrimination only. So it was that the Anilocrinae approximated to external attaching genera, Livonecinae to gill attaching while Ceratothoinae and Cymothoinae were buccal attaching.

The morphological distinction between Cymothoinae and Livonecinae has never been clear, and was based largely on pleon morphology. *Ichthyoxenus*

(Cymothoinae) has been considered by many authors to be a synonym of *Livoneca*. Similarly, Bowman & Tareen (1983) found little to differentiate *Catoessa* from *Livoneca*. Brusca (1981) had earlier recognised this, and placed all the gill and buccal attaching genera in a single lineage (see Brusca's fig.4B).

Good morphological data now exist for the Anilocrinae (Bruce, 1987a,b,c; Brusca, 1981; Bowman & Tareen, 1983; Williams & Williams, 1980, 1981, 1986, 1987), for *Mothocya* (Bruce, 1986), to a lesser extent *Ceratothoa*, *Glossobius* (Bruce & Bowman, 1989; Brusca, 1981), *Cymothoa* (Brusca, 1981, figures for *C. exigua*) and lastly the genera covered in the present study. There are many other contributions, but none has given figures for or described the pleopod morphology and most lack good drawings of mouthparts.

Using the descriptive data of the works just cited, plus the present work, a different and more complex pattern emerges, and the simple lineages illustrated by Brusca (1981) are no longer acceptable.

The pattern proposed is based on the premise that morphology takes precedence over location on the host in a classification. The second is that in many cases body shape is a convergent character, dependent on location on the host. Two examples of such body shape convergence are *Mothocya ihi* Bruce, a mouth parasitic species that looks superficially like other mouth attaching genera but by virtue of cephalic, pleonal and appendage morphology unambiguously belongs to *Mothocya*, all other species of which are gill parasitic. *Nerocila lomatia* Bruce is a gill parasite in a genus of otherwise externally attaching species. *Nerocila lomatia* converges with other gill attaching genera including an asymmetric body shape, pleonal processes reduced, flattened dorsum, and shortened coxae. There are presumably modifications imposed by the confined space of the gill cavity and gill arches. In both cases convergence has not obscured the generic affinity of each species.

The Anilocrinae was defined by Bruce (1987c). There are three genera in the present work, *Enispa*, *Livoneca* and *Norileca*, that show the anilocrine morphology of cephalon, pleon, brood pouch, pleopods, and clearly belong to this subfamily. To postulate the multiple independent evolution of trilobed cephalon, folded pleopods, and anilocrine brood pouch morphology is clearly less parsimonious than a monophyletic origin. The Anilocrinae, although primarily externally attaching, has genera that also use the buccal cavity (*Enispa*) and gill chamber (*Livoneca*, *Norileca*). The potential for members of this subfamily to use gill chamber and buccal attachment sites is easily understood when one sees anilocrine species attaching on the pectoral fin or head, and then in the case of *Nerocila lomatia*, actually in the branchial chamber.

The remaining genera can be separated into two or three groups these being equivalent to the Livonecinae, Cymothoinae and Ceratothoinae in the sense formerly used. Of these, those genera that attach to the gill arches can be clearly delineated, but at present have no nomenclatural standing as the name Livonecinae is herein synonymised with Anilocrinae. The Ceratothoinae can be unambiguously distinguished by antennular and antennal morphology, narrow anterior margin to the cephalon and operculate first pleopods. However, as it is not at all clear that these should be regarded as characters of subfamilial merit. The genera of the Ceratothoinae share an identical pleon and maxilla morphology with *Cymothoa*, type genus for Cymothoinae, and it is not possible to develop a clear conceptual difference between these two taxa at present.

Given that the morphological boundaries of most of the family group names proposed by Schiödte & Meinert are unclear, and that there still inadequate data for many cymothoid genera, it seems preferable to avoid the use of subfamily names other than Anilocrinae and Cymothoinae. It is premature to attempt a comprehensive new classification at present. More detailed morphological data is still needed and is becoming available for more genera. It should soon be possible to perform outgroup analysis, polarise the character states, and subject the family to cladistic analysis. Only by this method will the obscurities that exists within this family be resolved.

## Key to Australian Branchial-Attaching Cymothoid Genera

This key is handicapped by the lack of relevant descriptive data for the species of *Cterissa* Schiödte & Meinert, 1884, none of which have had their pleopods described. *Cterissa* is represented in Australia by a single species *C. australiensis* Avdeev, 1975. *Nerocila* Leach is usually an externally attaching genus but one species, *N. lomatia* Bruce, 1987, attaches in the branchial chamber of its host.

1. Coxae manifestly larger on one side than other ..... *Cterissa*

—— Coxae of about equal size on both sides ..... 2

2. Brood pouch without posterior pocket, pleopod rami all lamellar ..... 3

—— Brood pouch with posterior pocket, at least endopod of pleopod 5 with prominent lobes ..... 4

3. Antennule larger than antenna; maxilliped palp article 3 robust, without setae; pereopods with relatively long robust dactyli ..... *Mothocya*

—— Antennule shorter than antenna; maxilliped palp article 3 slender, with setae; pereopods with relatively short dactyli ..... *Elthusa*

4. Pleonites 1 and 2 with ventrolateral process; uropods extending beyond posterior of pleotelson ..... *Nerocila*

—— Pleonites 1 and 2 without ventrolateral processes; uropods not extending beyond posterior of pleotelson ..... *Norileca* n.gen.

## Taxonomy

### *Catoessa* Schiödte & Meinert

*Catoessa* Schiödte & Meinert, 1884: 309, 310.–Bowman & Tareen, 1983: 17.

**Type species.** *Catoessa scabricauda* Schiödte & Meinert, 1884, by monotypy.

**Provisional diagnosis of female.** Body strongly vaulted, bilaterally symmetrical, or weakly twisted to one side; about 2.5 times as long as wide. Cephalon weakly immersed in pereonite 1. Pleon narrow, not immersed into pereon; pleonite 1 narrower than 2; pleonites 2-5 subequal in width, lateral margins twisted, leaving gaps between pleonites.

Antennule subequal to, or longer than antenna, always more robust than antenna; bases set wide apart. Mandible palp slender; incisor noticeably elongate. Maxilliped without oostegital lobe. Pereopods without carina on basis, articles not dilated or expanded. Brood pouch arising from sternites 2-4 and 6. Pleopods all lamellar, rami rounded; endopods of pleopods 3-5 with simple proximomedial lobe.

**Composition.** *Catoessa boscii* (Bleeker, 1857), n.comb., *Catoessa gruneri* Bowman & Tareen, 1983 and *Catoessa ambassae* n.sp.

**Remarks.** Bowman & Tareen (1983) commented that there was little justification for separating *Catoessa* from *Livoneca*. In the light of new data on *Livoneca* presented here, there is clearly a great deal of difference between these two genera, although *Elthusa* and *Catoessa* have a similar pleopod morphology.

The type species is still not well known, and for this reason the diagnosis given here is provisional. Both *C. gruneri* and *C. ambassae* agree well on generic characters.

Examination of the types of *Livoneca boscii* (RMNH 67) show that it is an unequivocal member of *Catoessa*.

In Australia the genus is represented by the one species.

### *Catoessa ambassae* n.sp.

Figs 1, 2

**Type material.** HOLOTYPE, female (ovigerous 9.0), Lake Wooloweyah, Yamba, NSW, 19 Nov. 1984, in mouth of *Ambassis jacksoniensis* (AM I26537-09), collected by B. Ingram (AM P37761). PARATYPES, 9 females (ovigerous 7.5, 7.5#2, 7.8, 8.0, 8.5, 8.5#1, 9.3#3, non-ovigerous 7.5, 8.0), same data as holotype (AM P37762-P37766).

**Type locality.** Lake Wooloweyah, Yamba, NSW, about 29°00'S 153°19'E.

**Description of female.** Body about 2.5 times as long as wide, widest at pereonite 4; weakly ovoid, bilaterally symmetrical but twisted along longitudinal axis (giving asymmetric impression in dorsal view). Cephalon not deeply immersed in pereonite 1; eyes moderate, 0.36 width of cephalon; anterior margin produced, truncate, turned down, but not posteriorly. Coxae not conspicuous in dorsal view; coxae of pereonite 1 as long as segment; coxae 3-7 all shorter than respective segment. Pereonite 1<2<3<4>5>6>7; pereonites 6-7 decreasing abruptly in length, pereonite 7 being about half as long as 6. Posterior margin of pereonite 7 evenly indented. Pleon about 0.25 width of pereonite 4, not deeply immersed in pereon; all pleonites visible, pleonite 1 manifestly shorter than 2, pleonites 2-5 subequal in width. Pleotelson indented just posterior to articulation with pleonite 5, then widening; broadly rounded posteriorly.

Antennule robust, longer than antenna, composed of 8 articles; bases set wide apart. Antenna with 10 articles, extending to pereonite 1. Mandible incisor acute, elongate; palp articles all elongate, article 3 narrowing distally, with 4 distolateral spines. Maxillule with 4 terminal spines, 2 of which are distally recurved. Maxilla with single spine on lateral lobe, 2 on medial lobe. Maxilliped

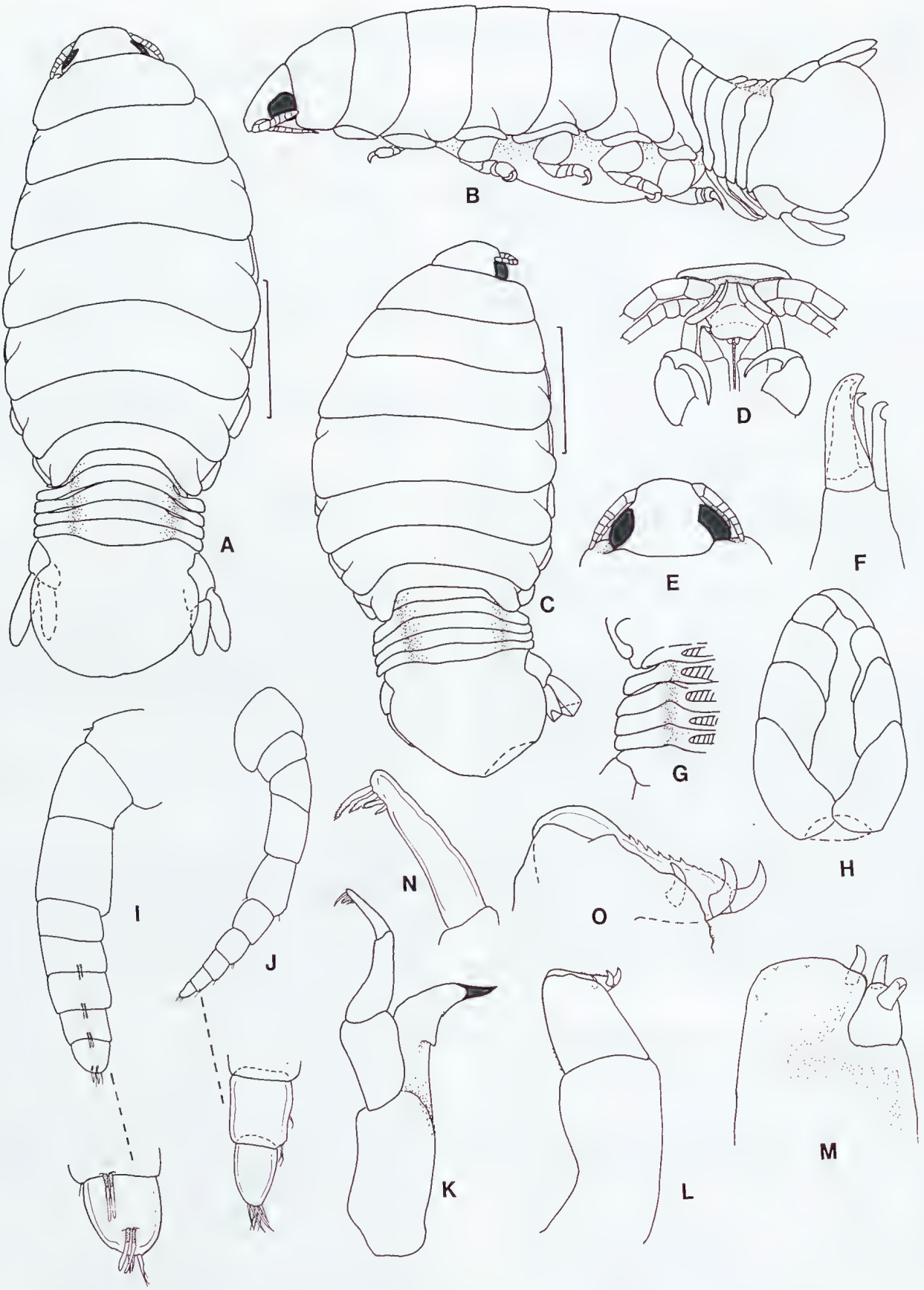


**Fig.1.** *Catoessa ambassae* n.sp. Figures of female #3 (AM P37765) except where indicated. A, dorsal view, holotype; B, lateral view, holotype; C, dorsal view, female #2 (AM P37764); D, frons, holotype; E, cephalon, holotype; F, maxillule apex; G, right pleonites, ventral view; H, brood pouch; I, antennule; J, antenna; K, mandible; L, maxilliped; M, maxilla apex; N, mandible palp article 3; O, maxilliped article 3. Scale lines represent 2.0 mm.

without laminar lobes; article 3 with 3 recurved spines.

Pereopod 7 slightly longer than 1. Pereopod 1 propodus short, about as long as combined lengths of merus and carpus; ischium about 0.32 length of basis. Pereopods 2 and 3 similar to 1. Pereopods 5-7 similar; pereopod 7 basis with carina, but not expanded; ischium about 0.7 length of basis. Brood pouch made up of 4 pairs of oostegites arising from coxae 2-4 and 6. No oostegites on coxae 1, 5 and 7.

Pleopods all lamellar, without folding or accessory lobes; endopods of pleopods 3-5 with proximomedial lobe. Peduncles 1-4 with 1-5 coupling hooks. Pleopod 1 shortest, exopod circular, exopods 4 and 5 slightly more elongate than 1. All pleopods with exopods longer than endopods. Uropod rami not exceeding posterior of pleotelson; endopod shorter than exopod, apices bluntly rounded.

**Male.** Not known.

**Colour.** In alcohol, tan, densely covered with chromatophores which extend onto ventral surfaces, antennule, antenna, pereopods and pleopods.

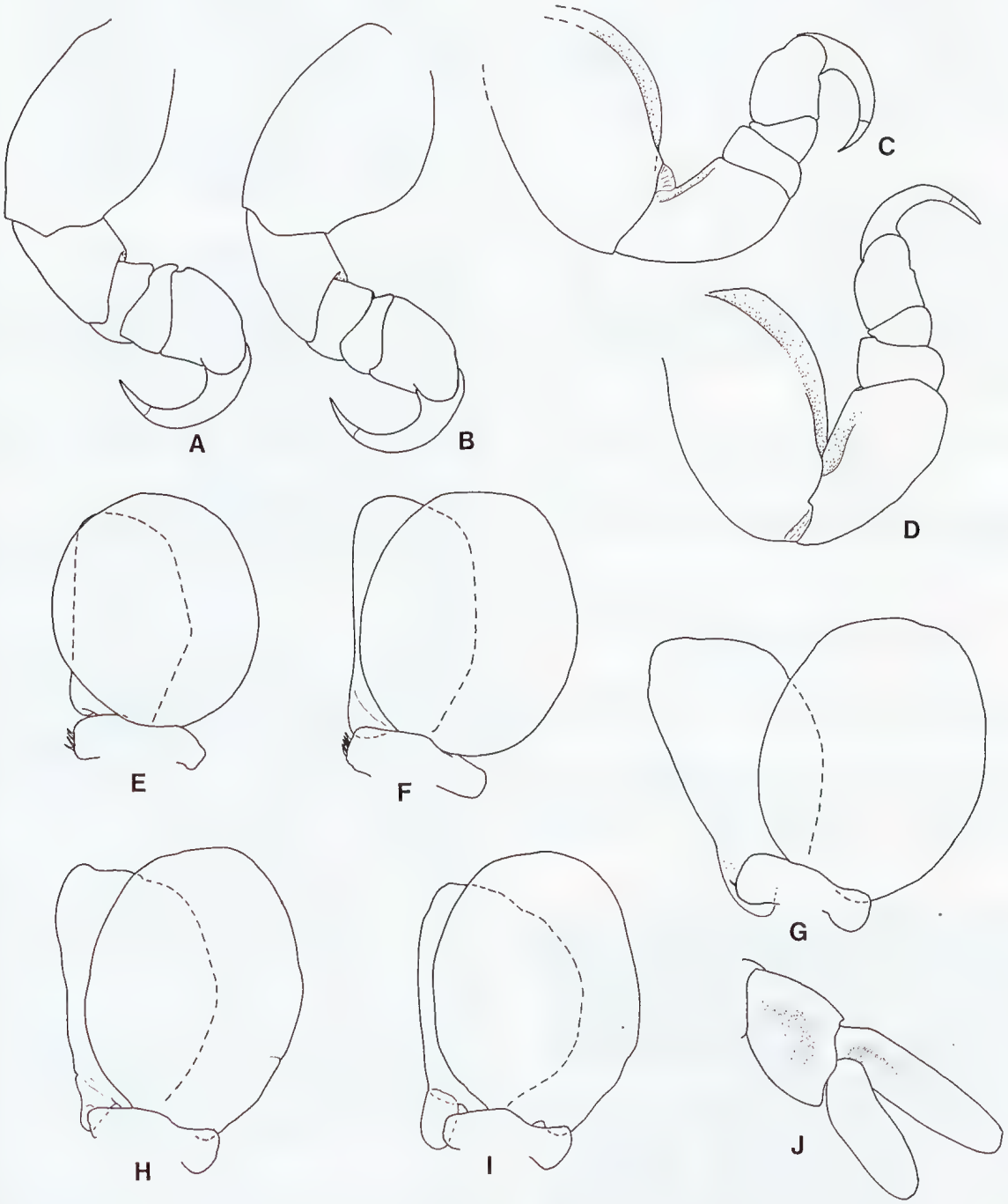


**Fig.2.** *Catoessa ambassae* n.sp. All figures of female #3 (AM P37765). A–D, pereopods 1, 2, 6, 7 respectively; E–I, pleopods 1-5 respectively; J, uropod.

**Size.** Mean size for ovigerous female 8.26 mm (n = 8).

**Variation.** The degree to which the body is rotationally twisted about its axis varies between specimens. The two immature females (lacking penial processes or appendix masculina) are noticeably more slender than ovigerous females (about 3.0 versus 2.5 times as long as wide).

**Remarks.** This species is readily distinguished from all other Australian cymothoids by the rotational twisting of the body. *Catoessa ambassae* is distinguished from others of the genus by the presence of a truncate rostrum coupled with a broadly rounded pleotelson. *Catoessa boscii* has a triangular pleotelson, *C. scabricauda* has an acute rostral point and *C. gruneri* has a rounded rostral point and posteriorly narrowed pleotelson.

**Host.** Present material is all from *Ambassis jacksoniensis* an estuarine species. The mode of attachment of isopod to host appears not to have been previously recorded. This isopod is a buccal parasite, but attaches to the lateral internal face of the buccal cavity, with the isopod dorsal surface medial. The head (in preserved specimens) projects beyond the host's mouth.

**Distribution.** Recorded only from the type locality.

**Etymology.** The specific name is taken from that of the host genus.

## *Elthusa* Schiödte & Meinert

*Elthusa* Schiödte & Meinert, 1884: 337.

**Type species.** *Livoneca emarginata* Bleeker, 1857, by monotypy (Schiödte & Meinert, 1884). One female syntype is held at the Rijksmuseum von Natuurlijke Historie, Leiden.

**Provisional diagnosis of female.** Body weakly vaulted, symmetrical or weakly twisted; about 1.8–2.3 times as long as wide. Cephalon moderately to strongly immersed in pereonite 1; posterior margin not trilobed. Pleon moderately to deeply immersed into pereonite 7, usually wide (greater than 0.5 width of pereon); pleonite 1 as wide, or only a little narrower than 2.

Antennule shorter than antenna; bases never in contact, varying from close set to wide apart. Mandible palp slender; article 3, or 2 and 3 with setae. Maxilliped with oostegital lobe. Pereopods with carina on basis; pereopods 1-3 with carpus cleft, receiving dactylus apex. Brood pouch arising from sternites 1-4 and 6. Pleopod rami all lamellar, without lobes or folding, progressively decreasing in size from pleopod 1 to 5. Pleopod 5 endopod rounded, or with straight medial margin, never indented.

**Composition.** All new combinations: *Elthusa atlantniroi* (Kononenko, 1988); *Elthusa californica* (Schiödte & Meinert, 1884), *E. caudata* (Schiödte & Meinert, 1884), *E. foveolata* (Hansen, 1897), *E. frontalis* (Richardson, 1910), *E. intermedia* (Nierstrasz, 1937), *E. menzeisi* (Brusca, 1981), *E. methipia* (Schiödte & Meinert, 1884), *E. nanoides* (Stebbing, 1905), *E. neocytta* (Avdeev, 1975), *E. ochotensis* (Kussakin, 1979), *E. philippinensis* (Richardson, 1910), *E. propinqua* (Richardson, 1904), *E. puhi* (Bowman, 1962), *E. raynaudii* (Milne-Edwards, 1840), *E. sacciger* (Richardson, 1909), *E. samariscii* (Shiino, 1951), *E. samoensis* (Schiödte & Meinert, 1884), *E. splendida* (Sadowsky & Moreira, 1981), *E. tropicalis* (Menzies & Kruczynski, 1983), *E. turgidula* (Hale, 1926), and *E. vulgaris* (Stimpson, 1857); also the new species described in this work *Elthusa myripristae* n.sp. and *Elthusa sigani* n.sp.

**Remarks.** Schiödte & Meinert (1884) gave a Latin diagnosis for *Elthusa* which, by contemporary standards, fails to differentiate the genus from other similar genera. The genus (and the type species) has received no attention since it was established. With the redefinition of *Livoneca* in this present work, and the re-examination of the types of *Elthusa emarginata*, it became apparent that most valid species that were in the past placed in *Livoneca* would be better placed in *Elthusa*.

The principal characters by which *Elthusa* can be identified are the weakly vaulted body shape, cephalon posterior margin not trilobed, a usually wide pleon, antennule shorter than antenna and all pleopods lamellar.

The diagnosis given here is provisional because the fragility of the holotype of the type species did not allow for dissection. The mouthpart and pleopod details given in the diagnosis are derived from the Australian species of *Elthusa*. However, although I could not examine the pleopods of *E. emarginata* in detail, they are all lamellar.

The genus as currently composed is more varied than other large cymothoid genera (e.g. *Anilocra*, *Nerocila*, *Mothocya*), and most species of the genus need to be fully redescribed. Areas of variation are position of the antennule (close set to wide apart), width of the pleon (manifestly narrow in *E. sacciger*) and width of pleonite 5 (narrower than pleonite 4 in *E. neocytta* and *E. sacciger*). These characters are constant within the larger genera for which there exists good data, and it may well be that *Elthusa* as presently constituted is not monophyletic.

The inclusion of *Elthusa turgidula* must be regarded as provisional. Clearly it cannot be retained in *Livoneca*. The very narrow pereonite 1 together with the antennule being larger than the antenna suggests it may be reassigned to another possibly new genus. Further study of related genera is necessary before this step can be taken. At present it is best placed in *Elthusa* but regarded as *incerta sedis*.

## Key to Australian Species of *Elthusa*

Note that the key applies only to adult (preferably ovigerous) females, and for most qualitative characters (e.g. couplet 6) reference to the figures is essential.

1. Pleonite 1 manifestly narrower than pleonite 2 ..... *E. turgidula*

—— Pleonite 1 about as wide as pleonite 2 ..... 2

2. Pleon less than half as wide a pereon maximum width; posterior coxae bulbous ..... *E. sacciger*

—— Pleon about 72–83% maximum width of pereon; posterior coxae not bulbous ..... 3

3. Pleonite 5 overlapped laterally by pleonite 4; body essentially bilaterally symmetrical ..... *E. neocytta*

—— Pleonites all subequal in width, body twisted to one side ..... 4

4. Cephalon with acute rostral point; posterior coxae small, not conspicuous in dorsal view ..... 5

—— Cephalon anteriorly rounded or truncate; posterior coxae prominent in dorsal view ..... 6

5. Pleonite 1 not visible in dorsal view; pleotelson about 4 times longer than visible pleon ..... *E. myripristae*

—— Pleonite 1 visible in dorsal view; pleotelson less than twice length of pleon ..... *E. propinqua*

6. Antenna longer than antennule; anterior margin of cephalon narrowly truncate (large size: 22–67 mm) ..... *E. raynaudii*

—— Antennule and antenna subequal in length; anterior margin of cephalon widely truncate (small size: 9–13 mm) ..... *E. sigani*

### *Elthusa myripristae* n.sp.

Figs3–5

**Material examined.** Female HOLOTYPE (ovigerous 26.0, AM P37773), male (12.5, AM P37774), Escape Reef, outer Barrier Reef 15°49'S 145°50'E, 29 Oct. 1981, on gills of *Myripristis violaceus*, depth 14-17 m (Fish No. I 22582-001), coll. J. Paxton, G. Allen *et al.*

**Description of female.** Body 1.9 times as long as wide, weakly twisted, widest at pereonite 3; dorsum weakly vaulted. Cephalon deeply immersed in pereonite 1, with distinct median rostral point; eyes 0.45 width of cephalon. Pereonite 1 longest, 6 and 7 shortest; coxae on pereonites 2 and 3 conspicuous in dorsal view, those of pereonites 4-7 short, in dorsal view partly or totally concealed by preceding pereonite. Posterior margin of pereonite 7 deeply indented. Pleonite 1 totally concealed by pereonite 7; pleonites 1-5 increasing slightly in width towards posterior. Pleon, at pleonite 5, 0.77 width of pereonite 3. Pleotelson 2.5 times longer than pleon, 0.70 as long as wide; widest medially.

Antennule with 8 articles, not extending to posterior of cephalon; bases set close together. Antenna longer than antennule, with 11 articles.

Mandible with mediodistal lobe and reduced molar; palp article 1 longest; palp article 3 half as long as 2, with

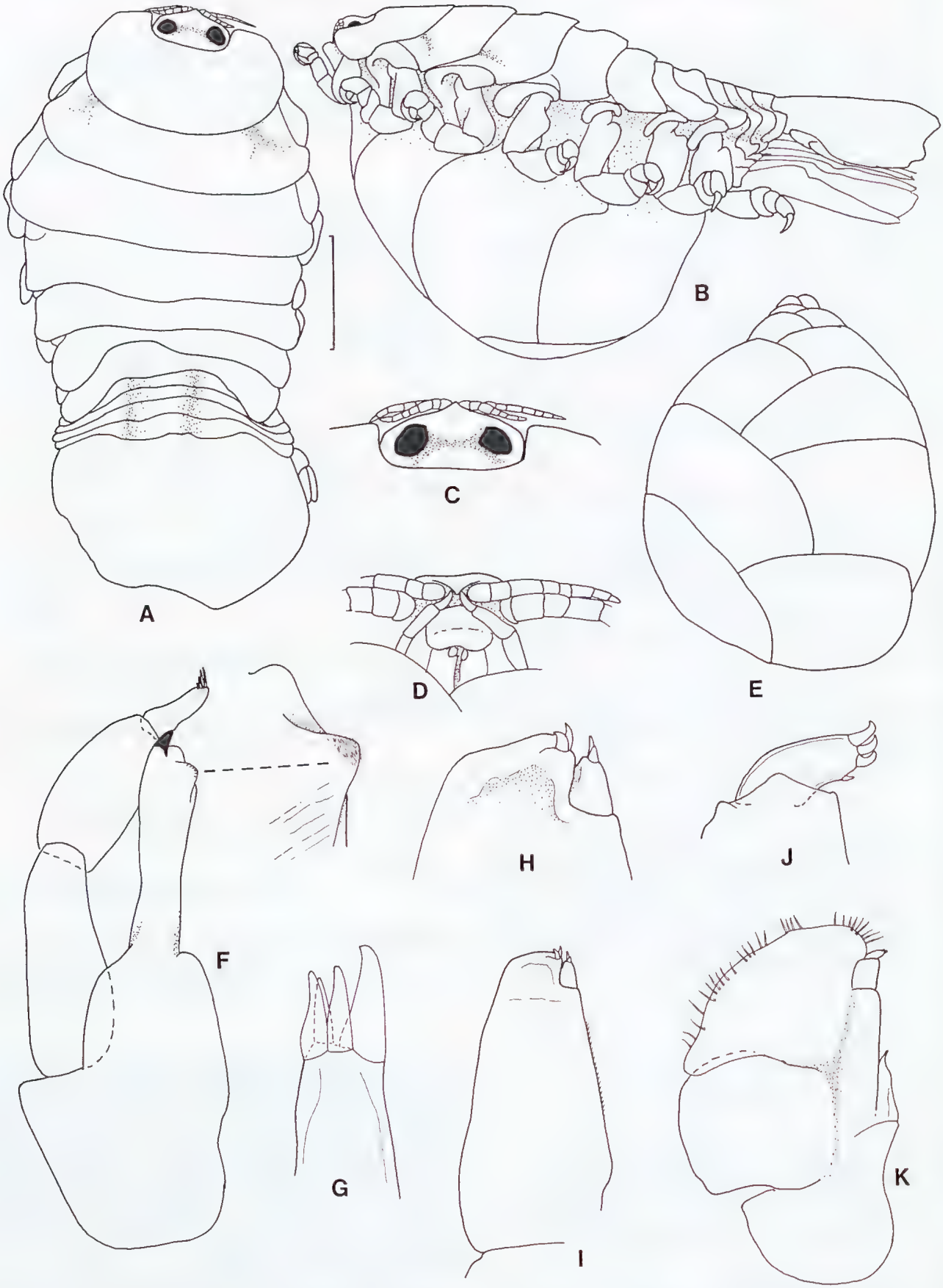


**Fig.3.** *Elthusa myripristae* n.sp. All figures of holotype. A, dorsal view; B, lateral view; C, cephalon; D, frons; E, brood pouch; F, mandible; G, maxillule apex; H, maxilla apex; I, maxilla; J, maxilliped article 3; K, maxilliped. Scale line represents 5.0 mm.

4 terminal setae. Maxillule with 4 terminal spines. Maxilla widening evenly from apex to base; medial and lateral lobes each with 2 spines. Maxilliped article 3 with 1 small and 3 large terminal spines.

Pereopods all with anterolateral carina on basis; dactylus short, extending to middle of carpus. Brood pouch deep, made up of alternately overlapping pairs of oostegites running from coxae 1 to 4 and 6; sternite 7 with 2 posteriorly placed submedian fleshy lobes.

Pleopod 2 exopod large, overlapping all other pleopods; endopods with proximedial lobe; peduncle with medial lobe. Pleopods 2-5 endopods with small, simple proximedial lobe; peduncles without medial lobes; exopods all with finely granulated patch on distomedial part of ramus. Uropods short, concealed by pleotelson in dorsal view; endopod slightly longer than exopod, margin converging to rounded apex; exopod lateral margin strongly curved.

**Male.** Dorsum more strongly vaulted than in female, lateral margins straight. Pleonite 1 totally concealed by pereonite 7. Pleotelson broadly rounded. Elongate paired penes on posterior of sternite 7.

Appendages similar to females except for mandible with longer molar; maxilliped articles 3 with larger spines; pleopods with longer peduncles; pleopod 1 peduncle

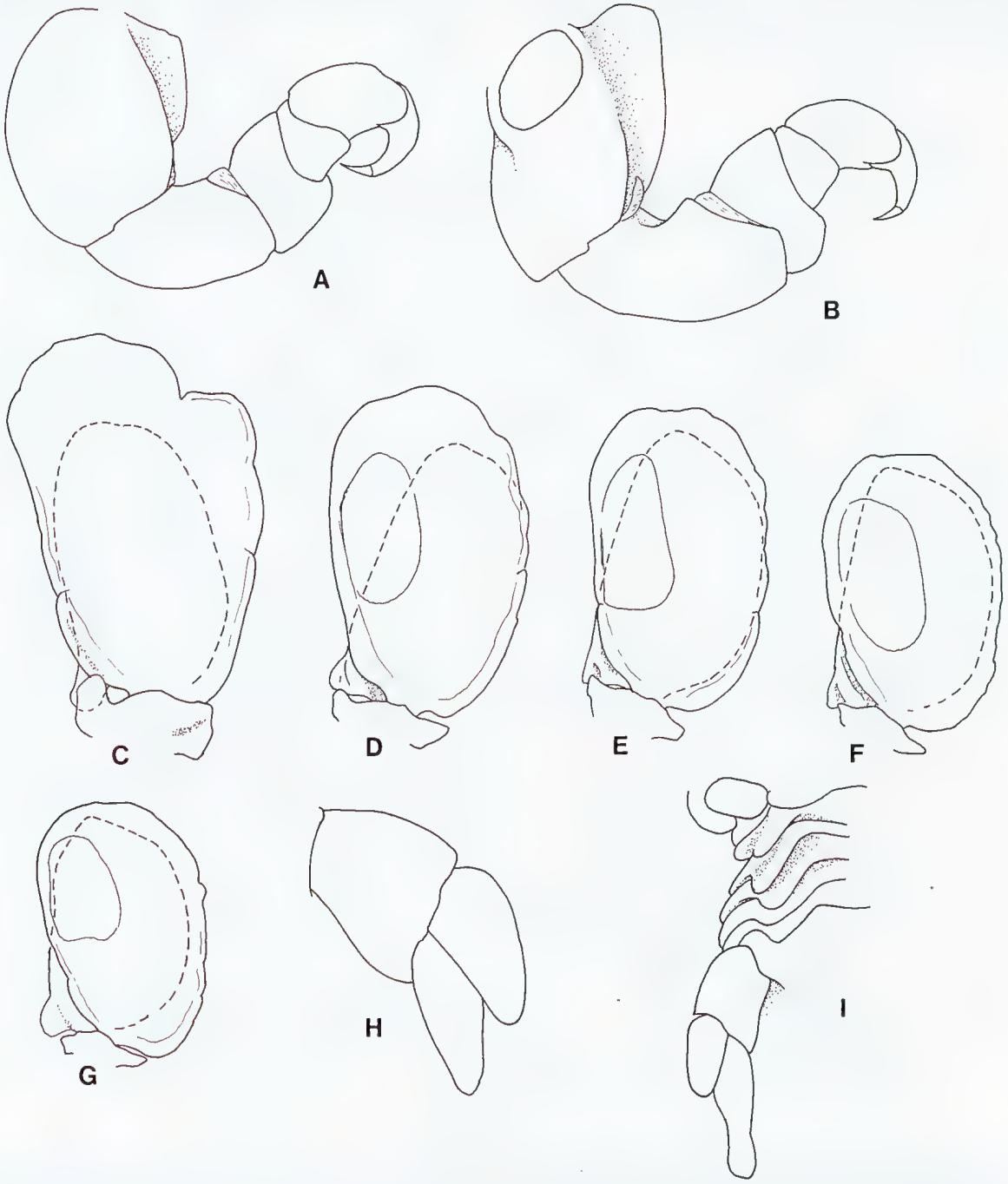


**Fig.4.** *Elthusa myripristae* n.sp. All figures of holotype. A, pereopod 1; B, pereopod 7; C–G, pleopods 1-5 respectively; H, uropod; I, right pleonites, ventral view.

without medial lobe; pleopod 2 with appendix masculina; uropod rami longer and wider.

**Colour.** Pale tan in alcohol, chromatophores not apparent.

**Remarks.** Two species show some similarity to *Elthusa myripristae*: *E. caudata* and *E. propinqua*. *Elthusa myripristae* can be separated from both these species by having pleonite 1 totally concealed in dorsal view by pereonite 7, and by the much smaller coxae on pereonites 4 to 7. *Elthusa propinqua* has a shorter pleotelson with uropods that extend beyond the posterior margin and differs in details of mouthpart, pereopod and pleopod morphology. Additionally *Elthusa propinqua* is a parasite of deepwater continental shelf and slope fishes. *Elthusa caudata* lacks the acute rostral point, but little else is known of this species. Avdeev (1978) listed *E. caudata* as occurring between Australia and New Zealand on *Genypterus blacodes* (Macruridae).

The mandible structure is apparently unique within the genus. Most cymothoids have a laminar molar; in *E. myripristae* this is reduced, and there are instead two small lobes adjacent to the incisor.

**Hosts.** Known only from *Myripristis violaceus*, attached abdomen innermost, at base of gill cavity.

**Distribution.** Escape Reef, northern Great Barrier Reef.

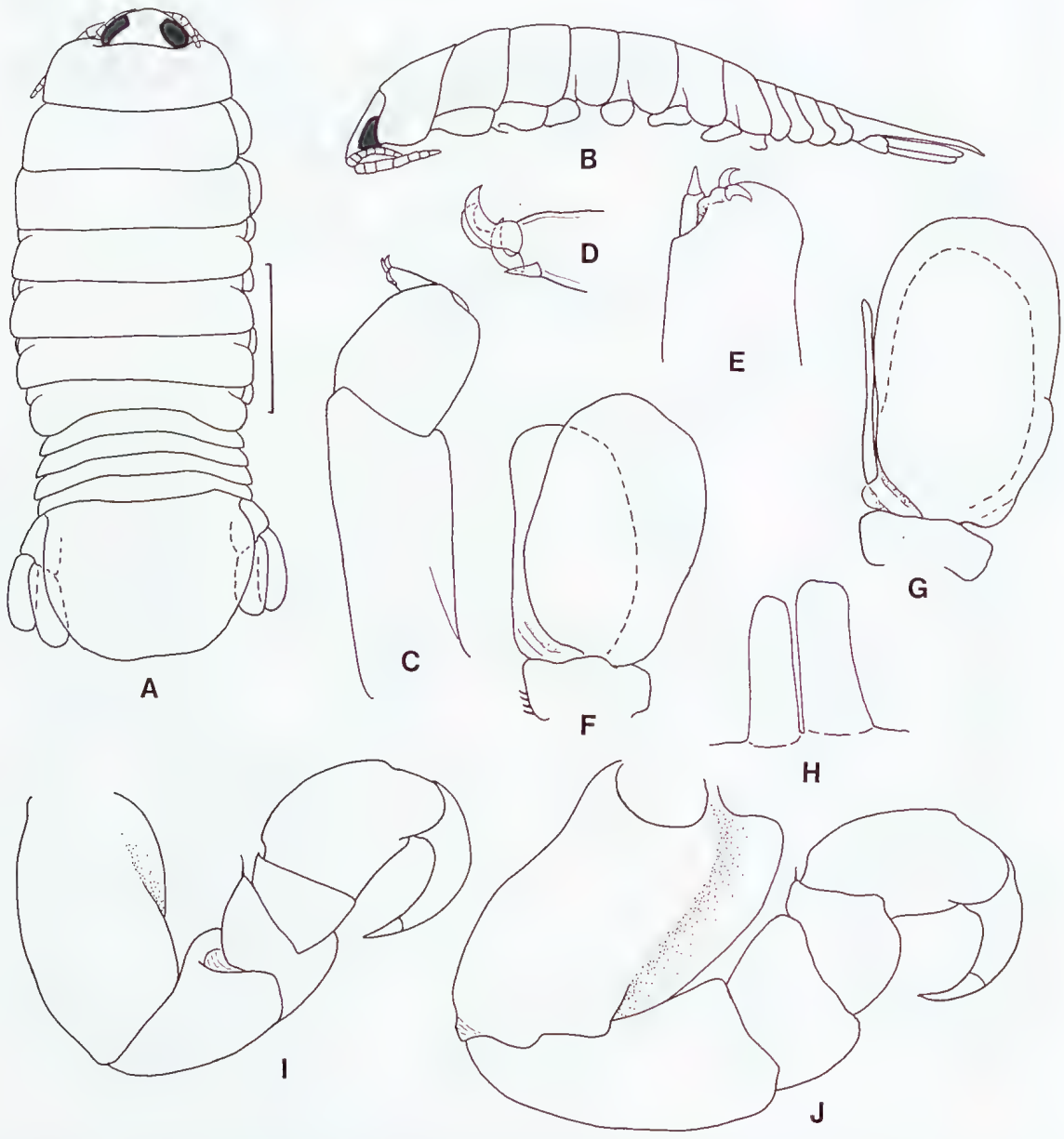


**Fig.5.** *Elthusa myripristae* n.sp. All figures of male paratype. A, dorsal view; B, lateral view; C, maxilliped; D, maxilliped article 3, apex; E, maxilla apex; F, pleopod 1; G, pleopod 2; H, penes; I, pereopod 1; J, pereopod 7. Scale line represents 3.0 mm.

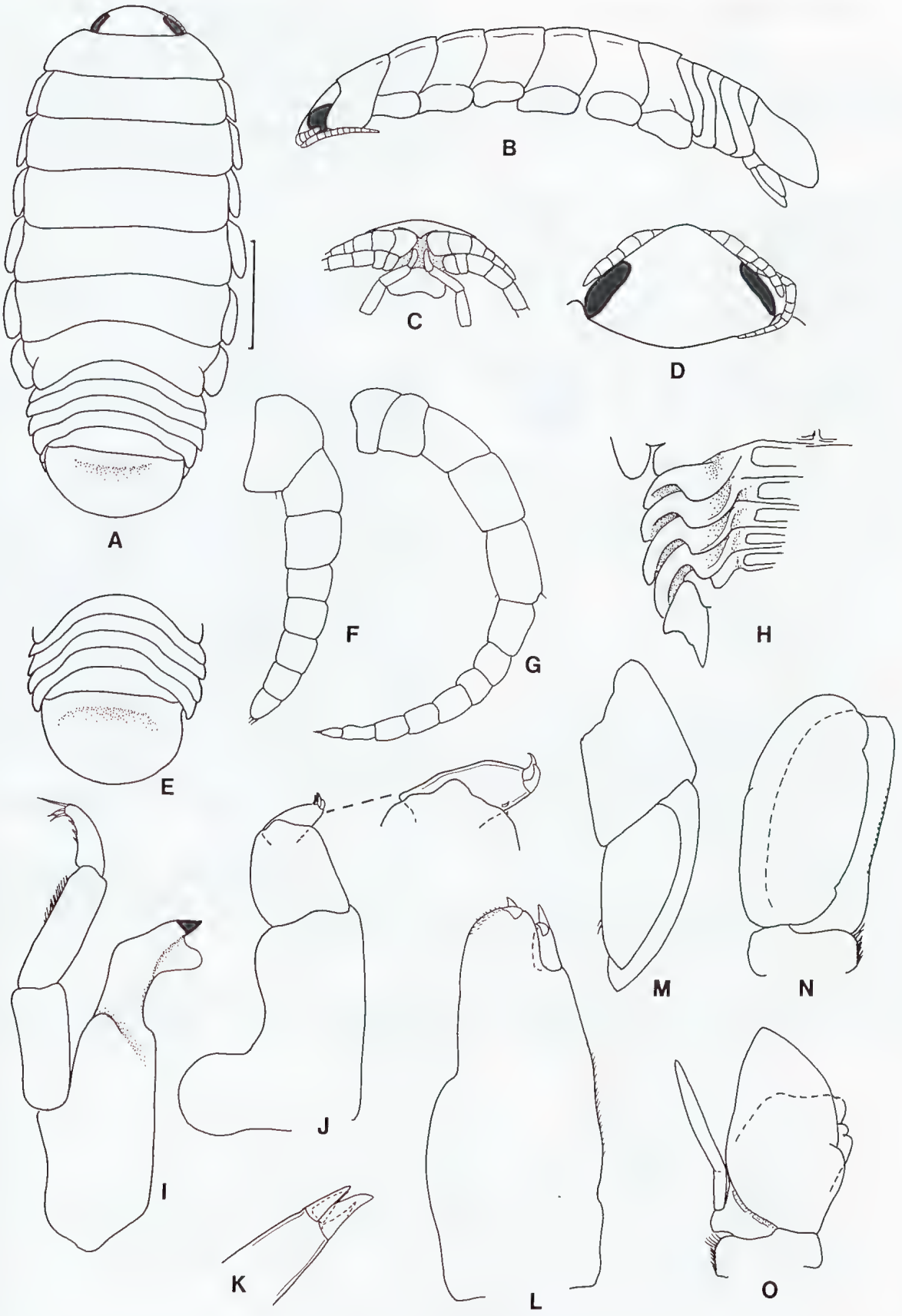


**Fig.6.** *Elthusa neocytta*. All figures of female 28.0 mm, Maria Island, Tasmania. A, dorsal view; B, lateral view; C, frons; D, cephalon; E, pleon and pleotelson, perpendicular view; F, antennule; G, antenna; H, right pleonites, ventral view; I, mandible; J, maxilliped; K, maxillule apex; L, maxilla; M, uropod; N, pleopod 1; O, pleopod 2 (damaged). Scale line represents 6.0 mm.

### *Elthusa neocytta* (Avdeev)

Figs 6, 7

*Lironeca neocyttus* Avdeev, 1975a: 247, figs 1, 2.
*Livoneca neocyttus*.–Stephenson, 1987: 135, 136, figs 1-10.

**Material examined.** All off Tasmania. Female (non-ovigerous 42.0), off Maria Island, 18 May 1983, in mouth of *Zenopsis nebulosus*, 443-456 m, coll. D. Coleman – CSIRO (AM P37769). Female (non-ovigerous 28.0), off Maria Island, 42°40.3'S 148°25.2'E, 1984, on gill of *Neocyttus rhomboidalis*, 494-504 m, coll. CSIRO – *Soela* (AM P37770). Female (non-ovigerous 26.0), off Strahan, January 1979, gill of *Neocyttus rhomboidalis*, about 600 m, coll. P.R. Last on *Zeehan* (AM P37772). Male/female (17.0), off Strahan, Jan. 1979, gill cavity of *Cyttus transversa*, coll. P.R. Last on *Zeehan* (AM P37771).

**Additional material.** 8 females (ovigerous 38.0, 41.0, 46.0, 53.0, 58.0, non-ovigerous 33.0, 55.0, 58.0), 13 males (17.0-29.0), north-east of East Sister Island, 39°16'S 148°44.0'E, 13 Oct. 1984, gills of *Neocyttus rhomboidalis*, 660 m, coll. W. Zeidler on *Soela* (SAM C4196).

**Type material.** Vladivostok, USSR (Avdeev, 1975a).

**Type locality.** New Zealand (Avdeev, 1975a).

**Description.** Body about 2.3 times as long as wide, lateral margins subparallel; dorsum moderately convex, with weak longitudinal median depression. Cephalon narrowing evenly to rostral point, triangular in dorsal view. Eyes 0.28 width of cephalon, elongate about 0.48 length of lateral margin. Pereonite 1=2<3<4>5>6>7; widest at pereonite 5.

Coxal plates all as long as respective segment, all conspicuous in dorsal view. Pleonites all visible; widest at pleonite 2 or 3, about 0.7 width of pereonite 5; pleonite 5 with lateral margins overlapped by pleonite 4. Pleotelson semicircular.

Antennule short, not reaching posterior of eye, with 8 articles. Antenna 1.6 as long as antennule, composed of 13 articles.

Pereopods without carina, bosses or dilated articles; pereopod 7 manifestly longer than 1.

Pleopods with all rami lamellar; lateral margins of peduncles 1-4 with coupling hooks. Pleopods 3-5 with endopod proximomedial lobe weakly developed. Uropods not extending beyond posterior of pleotelson, rami flat, endopod with blade-like margins, exopod slightly longer and narrower than endopod.

**Colour.** Pale cream, one specimen brown in alcohol. Eyes brown.

**Size.** Present material up to 58.0 mm. Avdeev (1975a) recorded the species up to 48.0 mm.

**Remarks.** The description is somewhat abbreviated here as there were no ovigerous females present at the time the description was made. All specimens had distorted pleopods.

Although differing in general appearance, *E. neocytta* shares several characters in common with *E. sacciger*. These are: pleonite 5 laterally overlapped by pleonite 4; pleopods all lamellar, with weakly developed endopod proximomedial lobe and with peduncular coupling hooks; pereopod 7 manifestly longer than 1; female maxilliped with 2 laminar lobes [Avdeev, 1975a, fig. 1(7)]; maxilla apically narrowed; mandible palp setose; antenna longer than antennule; and antennule bases close set.

*Elthusa neocytta* is easily identified by pleonite 5 being laterally overlapped by pleonite 4 and by the semicircular pleotelson. It is separated from *E. sacciger* by the very different body shapes, the wider pleon and the semicircular pleotelson.

The epithet has been emended to agree with the gender of the genus.

**Distribution.** Known from Tasmania at depths between 443 m and 660 m; common off south-eastern New Zealand at depths between 500 and 1100 m (Stephenson, 1987).

**Hosts.** In *Zenopsis nebulosus*, *Neocyttus rhomboidalis* and *Cyttus transversa* (all identified by Dr P.R. Last, CSIRO, Hobart).

**Fig.7.** *Elthusa neocytta*. Female, 28.0 mm, Maria Island. A, pereopod 1; B, pereopod 7.

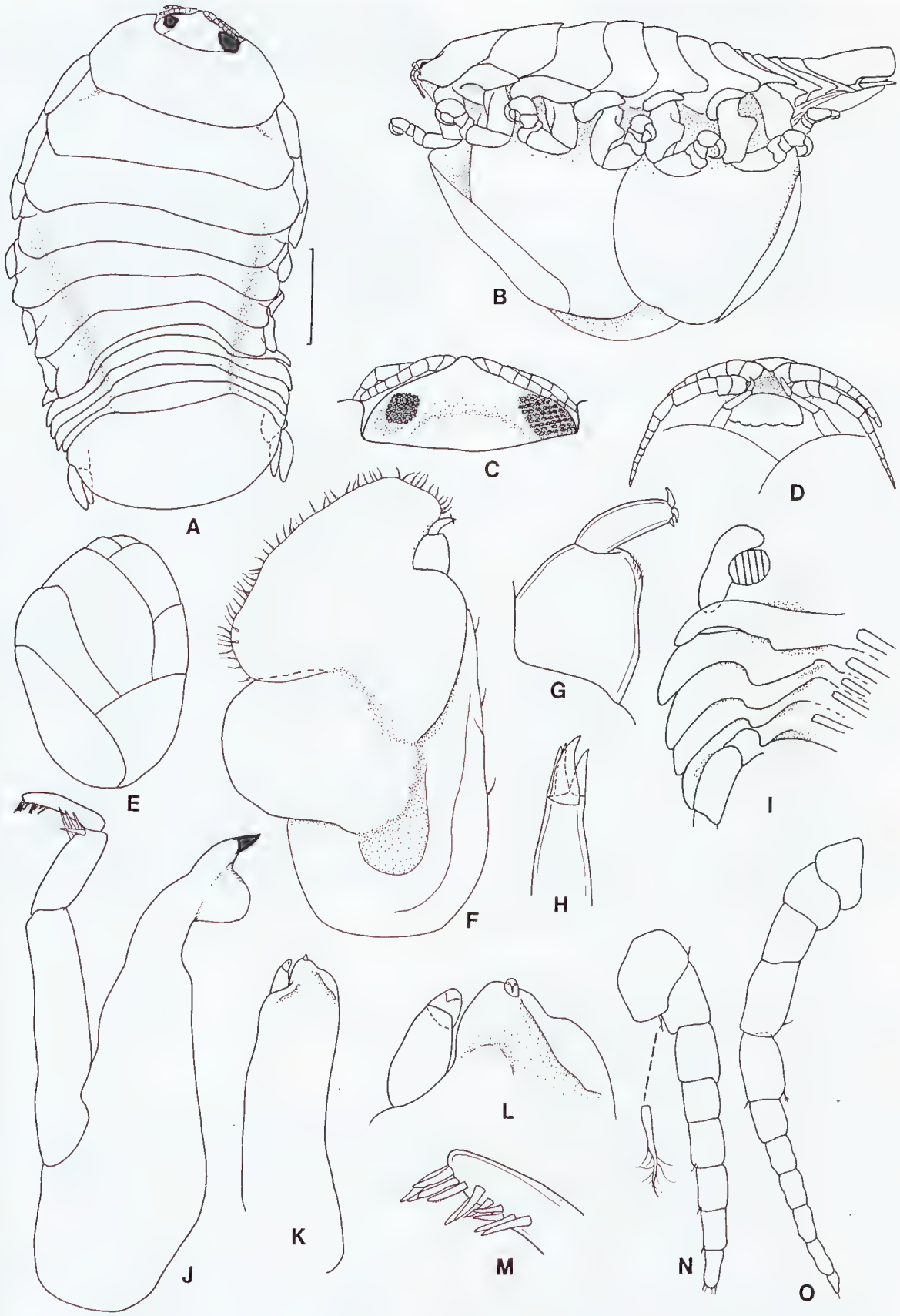


**Fig.8.** *Elthusa propinqua*. All figures female off Moreton Island (QM W11737). A, dorsal view; B, lateral view; C, cephalon; D, frons; E, brood pouch; F, maxilliped; G, maxilliped articles 2, 3; H, maxillule apex; I, right pleonites, ventral view; J, mandible; K, maxilla; L, maxilla apex; M, mandible palp article 3, apex; N, antennule; O, antenna. Scale line represents 3.0 mm.

### *Elthusa propinqua* (Richardson)

Figs 8, 9

*Lironeca propinqua* Richardson, 1904: 37, figs 6,7.–Richardson, 1909: 87; 1910: 23.–Thielemann, 1910: 42.–Nierstrasz, 1931: 143.–Barnard, 1936: 170.

**Material examined.** SYNTYPES, 3 females (ovigerous 22.5 [dissected, pereopods missing], 21.0, 13.5), Port Heda, Japan, Albatross Station 3738 (USNM 29086). Female (ovig 15.5), off Moreton Island, Qld, 27°56'S 154°00'E, 22 Mar. 1983, no host recorded, trawled 565 m, coll. R. Morton on *Iron Summer* (QM W11737).

**Additional material.** 3 females (ovigerous 15.0, non-ovigerous 10.5, 23.0), south-eastern Queensland, 23°23'S 153°22'E, Apr. 1988, on gills of *Ventrifossa* cf. *nigrodorsalis* (QM I25381), 500 m, coll. *Karumba Pearl* (QM W15431).

**Type locality.** Port Heda, Japan.

**Description.** Body 1.8-2.0 times as long as wide; dorsum with broad longitudinal ridge. Cephalon deeply immersed into pereonite 1, twice as wide as long, anterior margin with distinct median point; eyes occupying about 0.44 width of cephalon, facets distinct. Pereonite 3 widest, pereonites 4-7 becoming progressively narrower; all

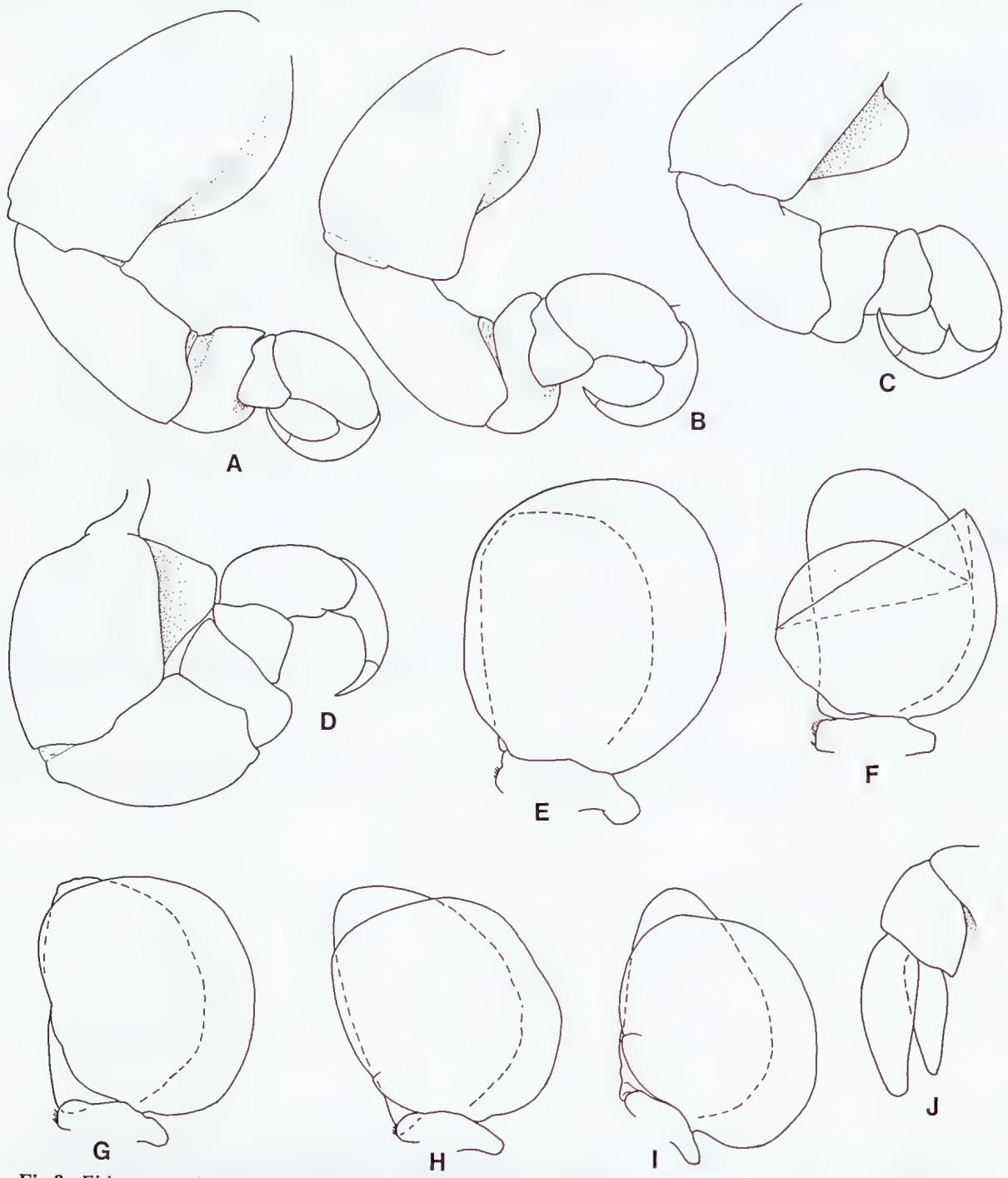


**Fig.9.** *Elthusa propinqua*. All figures of female, Moreton Island. A-D, pereopods 1, 2, 6, 7 respectively; E-I, pleopods 1-5 respectively; J, uropod.

coxae shorter than respective segment. Pleon 0.86 as wide as pereonite 3; pleonites all about equal in length, lateral extremities narrowed and bent posteriorly; pleonite 1 laterally overlapped by posterolateral angles of pereonite 7. Pleotelson 0.46 as long as wide, posterior margin smoothly curved.

Antennule bases close set, but not contiguous; composed of 8 articles, not extending beyond posterior of cephalon. Antenna bases set more widely apart; composed of 11 articles, extends to pereonite 2.

Mandible incisor acute, molar prominent; palp article 1 about 3 times as long as article 2; palp article 2 with 4 distolateral setae, palp article 3 with 12 stout distolateral spines. Maxillule with 4 terminal spines, one of which is slender. Maxilla with single spine each on medial and lateral lobes. Maxilliped article 3 with 3 weakly recurved spines.

Pereopod 1 longest, pereopods 2-7 progressively decreasing in length. Pereopod 1 basis with smoothly curved anterolateral carina; ischium about 0.7 as long as basis; dactylus curving smoothly. Pereopods 2 and 3 similar to 1, but basis with weak carina. Pereopods 4-7 basis anteromedial margin with proximal carina, increasing in size towards posterior. Pereopod 7 ischium 0.82 as long as basis.

Brood pouch made up of alternately overlapping oostegites arises from coxae 1-4 and 6; oostegites of coxae 1 overlapping mouthparts.

Pleopods all lamellar, all exopods approximately circular, and larger than endopods. Endopod of pleopod 1 subrectangular; endopods of pleopods 2-5 with distal apex becoming increasingly acute; endopods of pleopods 3-5 with proximomedial lobe weakly developed. Peduncles without lobes, medial margin of peduncles 1-4 with coupling hooks. Uropods short, not reaching posterior of pleotelson; peduncle 1.2 times as wide as long; exopod curving medially, lateral margin convex, apex bluntly rounded, endopod lateral margin straight, apex bluntly rounded.

**Male.** Not known.

**Colour.** Pale tan in alcohol; eyes orange.

**Size.** Present material 13.5-22.5 mm.

**Remarks.** *Elthusa propinqua* has been taken only from moderately deep water, and can be identified by the short cephalon (with moderately large eyes) with an acute rostral point, wide pleon, short uropods, close set antennules and the distinctive basis on pereopods 4 to 7.

**Hosts.** Recorded from "chalinura" (Richardson, 1909) in Japan, "a macrurid" (Richardson, 1910) in the Philippines, and from the gills of *Macrurus* in India (Barnard, 1936). The present material is from *Ventrifossa* cf. *nigrodorsalis* (identified by Mr J. Johnson, QM), family Macrouridae.

**Distribution.** Several localities in Japan, (Richardson, 1904, 1909) and the Philippines (Richardson, 1909), now from eastern Australia. Recorded at depths between 340 m to 835 m, the maximum depth being recorded by Barnard (1936).

### *Elthusa raynaudii* (Milne-Edwards)

Figs 10–12

*Livoneca Raynaudii* Milne-Edwards, 1840: 262.–Krauss, 1843: 66.–Schiödte & Meinert, 1884: 367, pl.12, figs 9-13.–Thielemann, 1910: 42.

*Cymothoa Novae-Zealandia* White, 1847: 110, *nomen nudum*.

*Lironeca novae-zealandia* Miers, 1874: 228.–Miers, 1876: 106, pl.III, fig.2.–Miers, 1881: 64, 67.

*Lironeca laticauda* Miers, 1877: 677, pl.69, fig.5.–Ellis, 1981: 124.

*Livoneca Raynaudi*.–Gerstaecker, 1882: 259.

*Livoneca Novae Zelandiae*.–Gerstaecker, 1882: 263.

*Lironeca Stewarti* Filhol, 1885: 450, pl.4, fig.6.

*Lironeca neo-zelanica*.–Thomson & Chilton, 1886: 154.

*Livoneca raynaudii*.–Whitelegge, 1902: 236.–Stebbing, 1910: 125.–Chilton, 1909: 606.–Chilton, 1911: 309.–Chilton, 1912: 135.–Young, 1926: 283.–Hale, 1926: 215, fig.10.–Hale, 1929: 261, figs 253, 259. –Hale, 1940: 303.–Barnard, 1940: 491.–Hurley, 1961: 268.–Hewitt & Hine, 1972: 108.–Sivertsen & Holthuis, 1980: 34.–Beumer, *et al.*, 1982: 33.

*Livoneca epimerias* Richardson, 1909: 88, fig.13.–Kussakin, 1979: 301, figs 69, 170.

*Livoneca raynaudi*.–Nierstrasz, 1915: 97.–Nierstrasz, 1931: 145.–Barnard, 1920: 358.–Pillai, 1954: 16.

*Livoneca laticauda*.–Nierstrasz, 1931: 143.

*Lironeca raynaudii*.–Brian & Dartevelle, 1949: 176.–Avdeev, 1975: 250.–Avdeev, 1978: 281.–Trilles, 1976a: 778, pl.1, fig. 4; Poore, 1981: 341.

*Lironeca raynaudi*.–Menzies, 1962: 115, fig.36A-B.–Kensley, 1978: 80, fig.33B.–Moreira & Sadowsky, 1979: 111.

*Lironeca magna* Mañé-Garzón, 1979: 18, figs 1-5.

**Material examined.** Female (ovigerous 31.5), off Capricorn Group, south-eastern Queensland, 22°56.7'S 152°12.3'E, 3 Oct. 1980, 342-360 m, on gills of *Physiculus* sp. (QM I18534), coll. QFS on *Graigmin* (QM W10250). Female (ovigerous 67.0 mm), north-east of Wollongong, NSW, 34°21-14'S 151°24-28'E, 3 Aug. 1975, 402 m, on fish, coll. FRV *Kapala* (AM P21037). Female (non-ovigerous 48.0), south-east of Gabo Island, Vic., 10 Nov. 1975, on *Zenopsis nebulosus*, coll. NSW SF on FRV *Kapala* (AM P20821). Tasmania, all coll. CSIRO: Female (non-ovigerous 31.5), male (14.0), Eaglehawk Neck, 6 Aug. 1978, on gill of *Pseudolabrus tetricus*, 5 m depth, coll. P.R. Last (AM P37777). Female (non-ovigerous 47.0), male (14.0), Murdunna, 17 Oct. 1976, on gill of *Meuschenia freycineti*, coll. D. Coleman (AM P37778). Female (non-ovigerous 20.0), Murdunna, 17 Oct. 1976, gill cavity of *Pseudophycis bachus*, coll. D. Coleman (AM P37779). Female (non-ovigerous 30.0), off Strahan, Jan. 1979, on gill of *Cyttus transversa*, about 600 m depth, coll. P.R. Last (AM P37776). Female (non-ovigerous 29.0), Long Reef, Dunally, 14 July 1980,

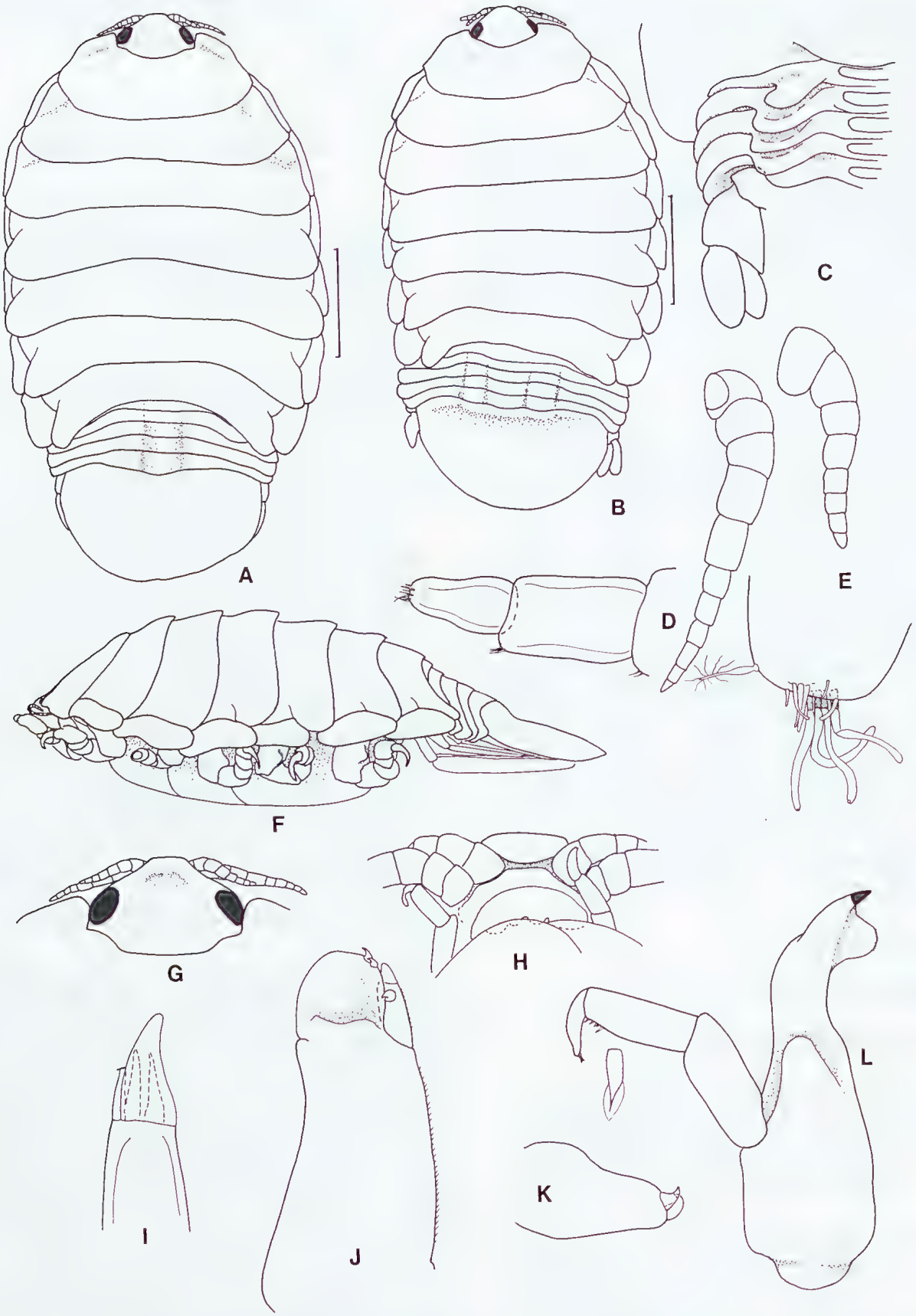


**Fig.10.** *Elthusa raynaudii*. All figures of Tarrana female, 31.0 mm (AM P37780) except B. A, dorsal view; B, AM G2181, off Coogee, NSW; C, right pleonites, ventral view; D, antenna and terminal article detail; E, antennule and detail; F, lateral view; G, cephalon; H, frons; I, maxillule apex; J, maxilla; K, maxilliped article 3; L, mandible. Scale lines represent 6.0 mm.

on gill of *Gnathanacanthus goetzei*, coll. P. Young, (AM P37775). Female (ovigerous 31.0), Flinder's Reef, Tarrana, Dec. 1981, on gill cover of *Pseudophycis bachus*, depth 10 m, coll. M. Hortle (AM P37780).

Female (ovigerous 47.0), Skua Point, Snares Islands, New Zealand, 1 Mar. 1972, mouth of *Pseudolabrus miles* (AM P30752).

**Additional material.** Material collected by F.I.S. *Endeavour*. Female, immature, Shoalhaven Bight, NSW, 16 Mar. 1909, 28-82 m (AM E288, E6598). Female, off Gabo Island, Vic., 12 Nov. 1913, about 366 m (AM E4762). Male, off Gabo Island, about 366 m (AM E4836). 2 females, Gabo Island to Everard, 37-366 m (AM E6319). Female, south-south-west of McCann, Vic., 128-183 m (AM E6318). 2 females, south-south-west of McCann, Vic., 27 Aug. 1914, 128 m (AM E5433). 2 females, eastern slope, Bass Strait (AM E6750). Female, off Tasmania (E6746). 2 females, east of Flinders Island, SA, (AM E6737). Male, south-east of Flinders Island, SA, 30 Aug. 1909, 68 m (AM E6743). Female, 80 km south of Cape Wiles, SA, 137 m (AM E4864). 4 females, 3 males, off

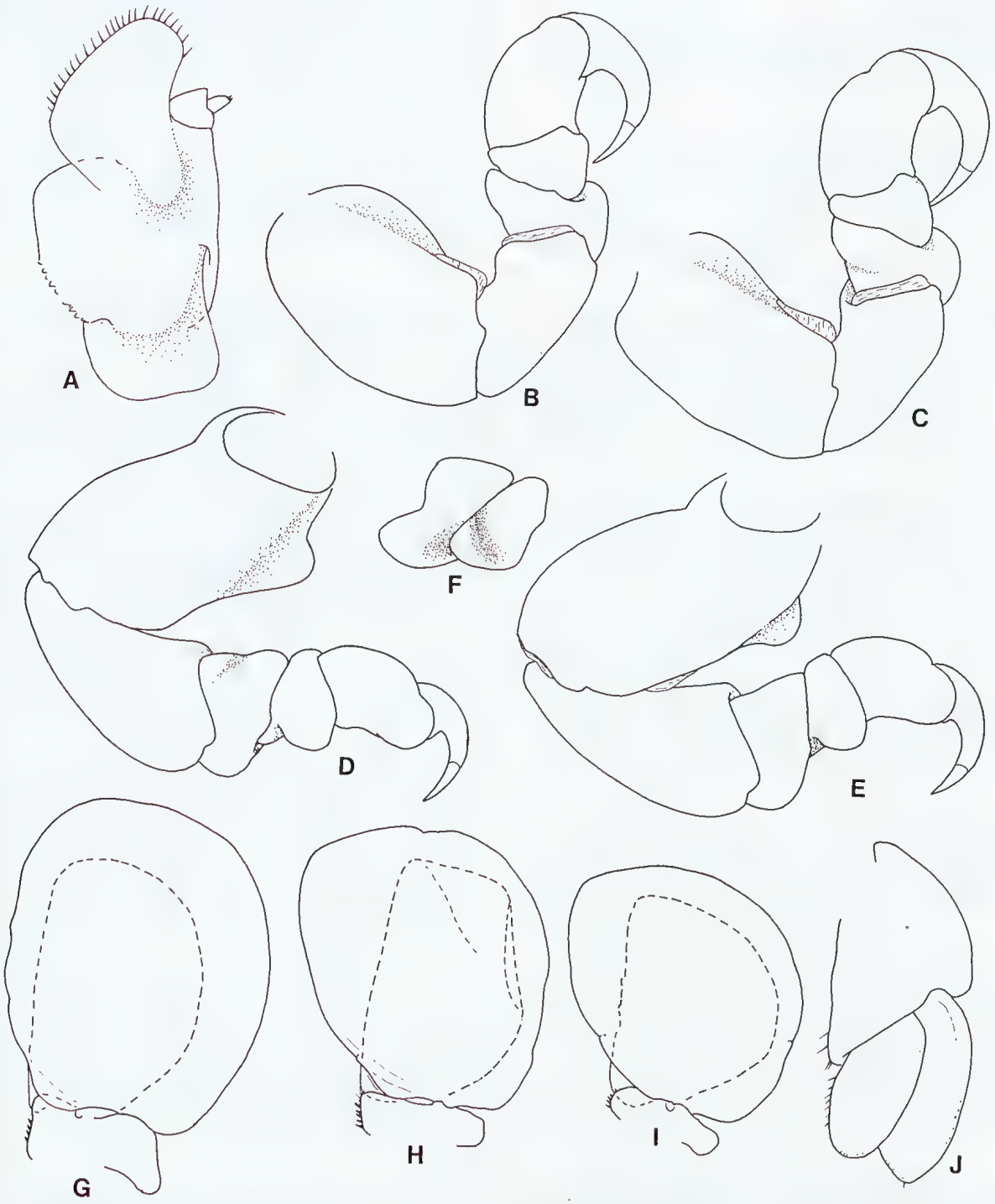


**Fig.11.** *Elthusa raynaudii*. All figures of Tarrana female. A, maxilliped; B–E, pereopods 1, 2, 6, 7 respectively; F, ventral view of merus and carpus, pereopod 7; G–I, pleopods 1, 2, 4 respectively; J, uropod.

west coast of Tasmania, 140 m, on banded perch (AM E5354). 5 females, 3 males, 2 immature, north-east of East Sister Island, 39°04'S 148°39'E, 13 Oct. 1984, gills of *Cyttus traversi*, 432 m coll. W. Zeidler or *Soela* (SAM C4197). 3 females, 8 males, north-east of East Sister Island, 39°21'S 148°46'E, 12 Oct. 1984, gills of *Cyttus traversi*, 476 m, coll. W. Zeidler, or *Soela* (SAM C4198). Female, off Tasman Head, Bruni Island, 21 Mar. 1914, 128-182 m (AM E6597). 3 females, entrance to Oyster Bay, Tasmania, 30 July 1909 (AM E5684). Female, off Iron Port, Storm Bay, Tasmania, 16 Mar. 1909, off operculum of *Zeus australis* (AM E4854).

HMCS *Thetis* series: 6 females, male, listed as from stations 2, 38 and 42, 9 km east of Cape Three Points, NSW, 33°34'S 151°20'E, 19 Feb. 1898, 65 (also 34°07'S 151°12'E, 12 Mar. 1898, 91 m, and 34°12'S 151°13'E, 13 Mar. 1898, 133 m) (AM P3328). Female, 9 km east of Coogee, NSW, 33°57'S 151°21.5'E, 15 Mar. 1898, 89 m, Stn 44 (AM G2181).

New South Wales: female, Terrigal 33°27'S 151°27'E (AM P4903). Female, Port Jackson, old collection (AM P5821). 2 females, off Botany Bay, 33°59'S 151°12'E, Aug. 1921, 60-102 m, coll. McNeill and Livingstone on *Goonambee* (AM P5426). 2 females, off Botany, Mar. 1927, 73 m, coll. A. Ward on *Bar-ea-mul* (AM P8820). 3 females, off Botany, Oct. 1926, 61 m, coll. A. Ward on *Gunner* (AM P8751). Immature female, off Watamooli, 34°00'S 151°10'E, Oct. 1924, on deck of trawler *Thistle*, coll. C.W. Mulrey (AM P9605). Immature female, male, off coast between Merimbula and Tathra, Mar. 1927, from flathead, coll. A. Ward on *Bar-ea-mul* (AM P8812). Female, male, 13 km south of Green Cape, 20 July 1925,

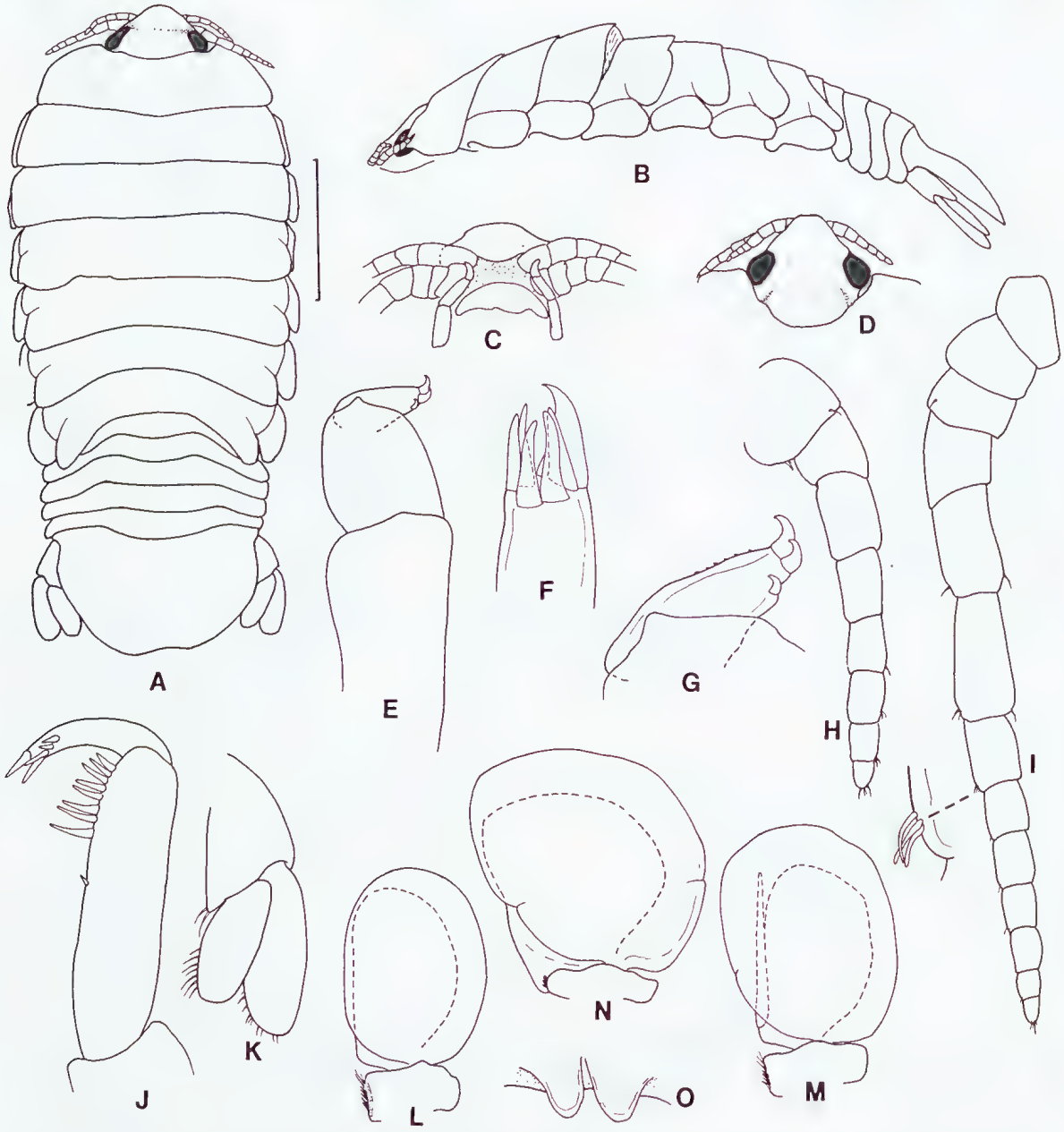


**Fig.12.** *Elthusa raynaudii*. All figures of male 14.0 mm Murdunna (AM P37778), except N. A, dorsal view; B, lateral view; C, frons; D, cephalon; E, maxilliped; F, maxillule apex; G, maxilliped article 3; H, antennule; I, antenna; J, mandible palp articles 2, 3; K, uropod; L, pleopod 7; M, pleopod 2; N, pleopod 5, – Tarrana; O, penes. Scale line represents 3.0 mm.

54 m, coll. N. Boardman on *Bar-ea-mul* (AM P8231, P8236). 3 females, 29 km south of Montague Island, Mar. 1927, from John Dory, 91 and 109 m, coll. A. Ward on *Bar-ea-mul* (AM P8813, P8815). 2 females, off Eden, Apr. 1927, from flathead, 73 m, coll. A. Ward on *Bar-ea-mul* (AM P8825, P8827). 2 females, male, between Port Stephens and Jervis Bay, July 1980, on *Rexea solandri*, 282-457 m, on *Kapala* (AM P37282).

**Also examined.** Holotype of *Livoneca epimerias* Richardson (USNM 39504), syntypes of *Livoneca laticauda* Miers (BMNH 1862: 96).

**Type material.** I have not examined the type specimens of this species. Trilles (1976a) provided a photograph of *Elthusa raynaudii* but did not specify which of the specimens it was that he was illustrating. The types are held at the Muséum National d'Histoire Naturelle, Paris. Examination of the holotype of *Livoneca epimerias* Richardson (USNM 39504) failed to reveal any differences from material currently being identified as *E. raynaudii*.

**Type locality.** Cape Bonne-Espérance (collected by M. Raynaud), Cape of Good Hope, South Africa.

**Description of female.** Body ovate, symmetrical or weakly twisted, about 1.75 times as long as wide; widest at pereonite 5. Cephalon moderately immersed in pereonite 1, anterior margin produced, turned down; eyes 0.33 width of cephalon. Pereonites 1 and 5 longest; pereonite 1>2<3<4<5>6>7. Posterior margin of pereonite 7 evenly indented. Pleonite 1 largely concealed by pereonite 7; pleonite 1 slightly narrower than 2; pleonites 2-5 subequal in width. Pleotelson short, semicircular or flattened semiarc in shape.

Antennule shorter than antenna, bases set wide apart; composed of 8 articles. Antenna extending to pereonite 1, composed of 11 articles.

Mandible with prominent molar; palp with 5 and 2 setae on distolateral margin of articles 2 and 3 respectively. Maxillule with 1 broad and 3 narrow spines. Maxilla with 2 spines each on medial and lateral lobes respectively. Maxilliped article 3 with 2 terminal spines.

Pereopods increasing in length posteriorly. Basis of pereopods 1-3 with weak carina; dactylus not extending beyond carpus; carpus with posterior margin cleft. Pereopod 5-7 basis with carina most pronounced proximally. Brood pouch made of alternately overlapping oostegites arising from coxae 1-4 and 6. Sternite 7 with 2 submedian fleshy lobes on posterior margin.

Pleopods 1-5 becoming progressively smaller. Exopod manifestly larger than endopod on all pleopods. All pleopods with coupling hooks on peduncle medial margin; all rami lamellar; endopod proximomedial lobe weakly developed. Uropod exopod about as long as peduncle, slightly longer than endopod; both rami broadly rounded, not reaching posterior margin of pleotelson.

**Male.** Body lateral margin subparallel, about 2.2 times as long as wide. Pleon proportionally longer than in female.

Appendages similar to those of female but antenna proportionally longer and composed of 13 articles; mandible palp with more setae; maxillule with 1 broad and 5 slender spines; maxilliped article 3 with recurved spines; pereopods 5-7 proportionally longer and more slender than in female; pereopod 2 with spines at posterodistal angle of basis 1 ischium, merus, carpus and propodus; pleopod 2 with appendix masculina as long as endopod, arising sub-basally.

**Colour.** Pale brown or tan in alcohol, chromatophores not apparent.

**Size.** Ovigerous females 22.0-67.0 mm, mean 30.83 mm (n = 31); length/width 1.35-2.0 mm, mean 1.67 (n = 25). Non-ovigerous females 22.0-49.0 mm, mean 29.25 (n = 20); length/width 1.45-2.2 mm, mean 1.79 (n = 16). Males 14.0- 21.0 mm, mean 16.79 (n = 12); length/width 1.60-2.25 mm, mean 2.03 (n = 4).

**Variation.** The relative width of the pleon varies and a wider pleon is shown in Figure 16B (AM G2181). Very large specimens (48.0 mm, AM P20821 and 67.0 mm, AM P21037) have proportionally longer pleotelsons. Most specimens are symmetrical, occasionally an animal may be slightly twisted to the left or right.

**Remarks.** This species, described by Milne-Edwards (1840) from the Cape of Good Hope has been widely recorded in the southern oceans. From figures given, descriptive accounts and recorded host identities it seems probable that most records are accurate. The records of Pillai (1954) on clupeid hosts and Powell (1959, quoted in Stephenson 1969) on a hemiramphid should be regarded as doubtful.

*Elthusa raynaudii* is characterised by the wide anterior margin to the cephalon, large size, ovate body shape, short pleon and pleotelson, short uropods and the basis of pereopods 5-7 with the proximal part of the carina forming a boss.

Two other large species, *E. neocyttus* and *E. sacciger*, are easily distinguished by having the lateral margins of pleonite 5 completely encompassed by pleonite 4. In addition, *E. sacciger* has a prominently ovoid body with a very narrow pleon.

*Livoneca rafineskii* Leach, 1818, suggested by Trilles (1976) as the possible senior name for this species is a junior synonym of *Livoneca redmanii* Leach (see *L. redmanii*). *Livoneca laticauda* Miers, proved, on examination of the types, to be indistinguishable from *E. raynaudii*, as was so for *Livoneca epimerias* Richardson. The figures given by Mañé-Garzón (1979) for *Lironeca magna* also force the conclusion that it is a junior synonym of *E. raynaudii*.

*Livoneca ochotensis* Kussakin, 1979, is very similar to *E. raynaudii*, but Kussakin's figures show some slight differences. Without detailed redescription it is not possible to evaluate its status. Kussakin (1979) also

transfered Gurjanova's (1936) record of *E. raynaudii* to *L. ochotensis*. The occurrence of *E. raynaudii* in Japan (Richardson, 1909) suggests the status of *E. ochotensis* needs to be critically re-evaluated.

**Hosts.** Australian records: *Physiculus* sp., *Physiculus barbatus*, *Pseudophycis bachus* (F. Moridae); *Pseudolabrus tetricus* (F. Labridae); *Meuschenia freycineti* (F. Monocanthidae); *Gnathanacanthus goetzei* (F. Gnathanacanthidae); *Zenopsis nebulosus*, *Cyttus australia*, *Cyttus traversi* (F. Zeidae); *Rexea solandri*. Unidentified by scientific names: banded perch (F. Serranidae), flathead (F. Platycephalidae).

Other records have been summarised by Trilles (1976); see also Sivertsen & Holthuis (1980). New Zealand records have been summarised by Hewitt & Hine (1972), with additional records given by Poore (1981).

Pillai (1954) recorded *Pellona brachysoma* and *Stolopherus commersoni* and Powell (1959) recorded *Hemiramphus intermedius* as hosts (quoted by Stephenson, 1969), but these records require confirmation.

**Distribution.** The northernmost Australian record is from off the Capricorn Group, 22°S; common off the mid-New South Wales coast, Tasmania and Victoria; there are no records from South Australia and Western Australia. Also recorded (under several names) from New Zealand, South Africa, Uruguay, (Mañé-Garzón, 1979), southern Chile (Menzies, 1962), Tristan da Cuhna (Sivertsen & Holthuis, 1980).

### *Elthusa sacciger* (Richardson)

Figs13–15

*Livoneca sacciger* Richardson, 1909: 87, fig.12.–Gurjanova, 1936: 90,91, fig.45.–Shiino, 1951: 86, fig.2A.–Shiino, 1965: 544, figs 7, 27.
*Livoneca saccigera*.–Nierstrasz, 1931: 144 (lapsus).
*Lironeca sacciger*.–Kussakin, 1979: 300, fig.168.

**Material examined.** Female HOLOTYPE (ovigerous 33.0), off Mizimoko Light, Japan, 23 Aug. 1906, 786 m, Albatross Stn 4957, coll. U.S. Fish Commission Steamer *Albatross* (USNM 39503). 3 females (ovigerous 40.0, 39.0, 37.0), male (21.5), off Sydney, NSW, 33°43.0'S 152°1.5'E, 11 Oct. 1984, 995 m, coll. NSW State Fisheries *Kapala* (AM P37767). Female (35.0), 2 males (24.0, 17.0), off Sydney, NSW, 33 34.5'S 151 58'E, 21 Dec. 1976, 823 m, coll. NSW State Fisheries *Kapala* (AM P37768).

**Type locality.** Off Mizimoko Light, Japan.

**Description of Australian female.** Body 1.5-1.8 times as long as wide, bilaterally symmetrical, widest at pereonite 5; pereonite 1<2<3<4<5>6>7. Cephalon with rostral point; eyes about 0.2 width of cephalon. Coxae of pereonites 2-4 each shorter than respective segment; coxae of pereonites 5-7 project laterally, bulbous; posterior margin of pereonite 7 deeply indented. Pleon about 0.4-0.5 width of pereonite 5; pleonites 1 and 2 laterally overlapped by pereonite 7; lateral margin of pleonite 4 posteriorly directed, laterally overlapping pleonite 5. Pleotelson 0.7-0.8 times as long as wide, subtriangular to posteriorly rounded.

Antennule basal articles in contact; composed of 8 articles, extending to pereonite 1. Antenna bases set wide apart; composed of 12 articles, extending about halfway along pereonite 1; articles 4 and 5 distinctly longer than 1-3; articles 6-12 short, becoming progressively shorter.

Mandible palp articles 2 and 3 with abundant short setae on distolateral margin. Maxillule with 5 spines. Maxilla tapering distally, 2 spines each on medial and lateral lobes. Maxilliped with 2 laminar oostegital lobes; article 3 with 3 weakly curved spines.

Pereopods 1-3 manifestly shorter than 5-7; pereopods 5-7 with weak carina on basis. Pereopod 1 dactylus smoothly curved, extending to middle of carpus; dactylus of all pereopods with slender unguis.

Brood pouch made up of alternatively overlapping oostegites arising from sternites 1-5, anterior pair of oostegites overlapping mouthparts.

Pleopods all lamellar; pleopods 3-5 endopod proximomedial lobe weakly developed. Pleopod 2 with appendix masculina about 0.6 length of endopod. Peduncles 1-4 each with about 6 coupling hooks and with plumose setae. Uropod rami not extending beyond posterior of pleotelson; rami subequal in length, with subparallel margin and abruptly rounded to subtruncate apices.

**Male.** Body 2.5 times as long as wide, subparallel; pleon not immersed in pereonite 7. Eyes larger than female. Uropods extend beyond posterior of pleotelson. Antennule and antenna similar to female, but antenna extends to anterior of pereonite 2. Appendages similar to female but maxilliped article 3 with 4 hooked spines and mandible palp more setose.

Smallest male (swimming stage) with spinose pereopods, setose margins to the uropods and pleotelson, and with wide rounded uropodal rami.

**Colour.** Pale tan in alcohol.

**Size.** Females 33.0-40.0 mm; males 17.0-24.0 mm.

**Remarks.** This large species has numerous distinctive characters. Adult females are bilaterally symmetrical and distinctively ovoid in shape, the posterior coxae are bulbous, the pleon is short (about 0.12 as long as the body), pleonite 5 is overlapped by pleonite 4, pereopods 5 to 7 distinctly longer than 1 to 3 and pleopods 1 to 4 with large coupling hooks and plumose setae on the peduncle. There are no other similar species of *Elthusa*, and the bulbous coxae allows easy identification.

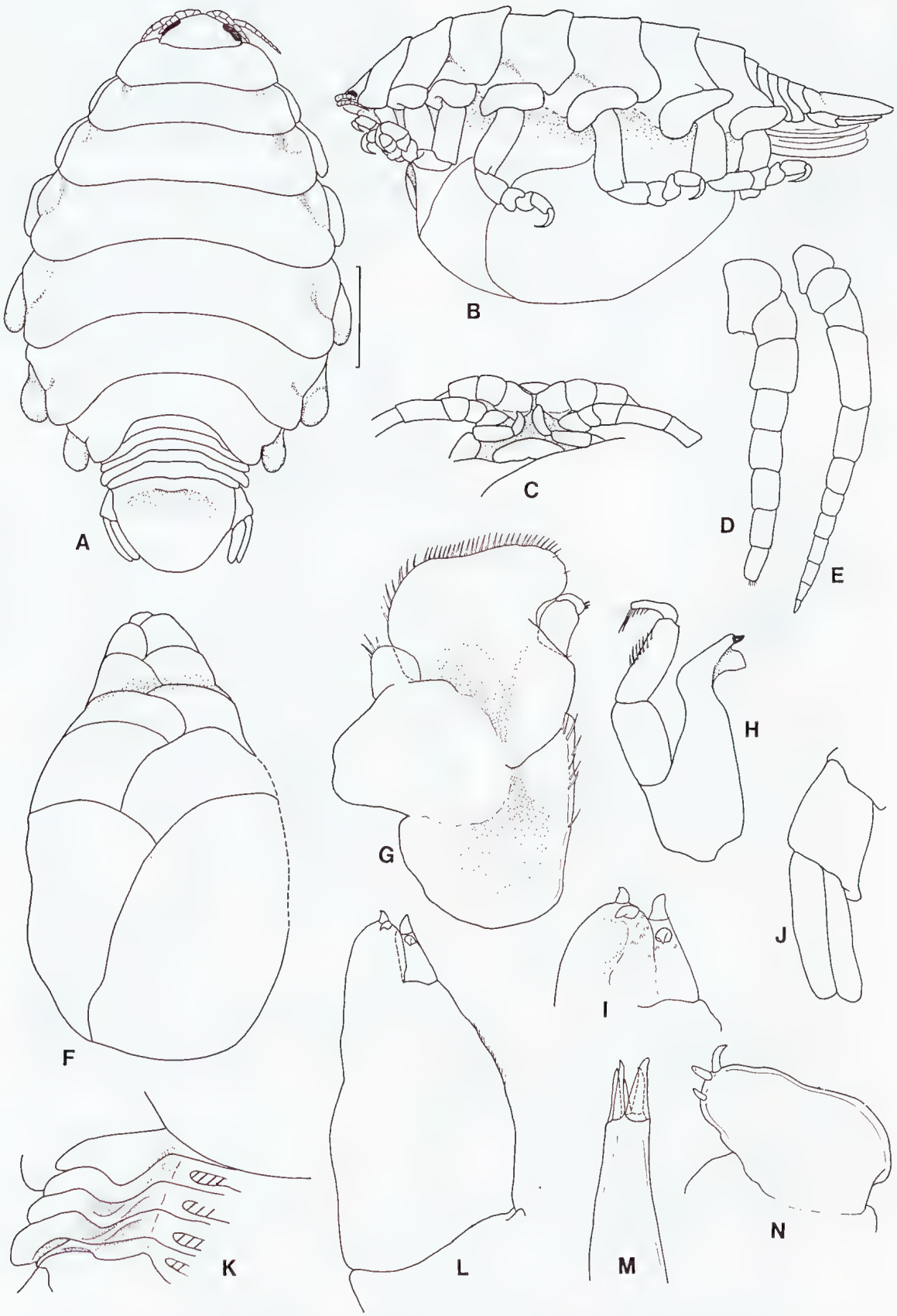


**Fig.13.** *Elthusa sacciger*. All figures of female, 39.0 mm except F. A, dorsal view; b, lateral view; C, frons; D, antennule; E, antenna; F, brood pouch, 37.0 mm; G, maxilliped; H, mandible; I, maxilla apex; J, uropod; K, right pleonites, ventral view; L, maxilla; M, maxillule apex; N, maxilliped article 3. Scale line represents 7.0 mm.

**Hosts.** Australian material lacked host data. Richardson (1909) recorded the species from "mouth of *Synaphobranchus*", and Shiino (1951) recorded the host *Synaphobranchus pinnatus*, Family Synaphobranchidae. These are 'cutthroat eels' which occur at depths between 200 and 3000 m.

**Distribution.** Previous records are all from Japan or north-western Pacific. Present material from off the central coast of New South Wales at the depths of 823 and 995 m.

### *Elthusa sigani* n.sp.

Figs 16–18

**Material examined.** Female HOLOTYPE (ovigerous

**Fig.14.** *Elthusa sacciger*. All figures of female 39.0 mm. A-D, pereopods 1, 2, 6, 7 respectively; E–H, pleopods 1-3, 5 respectively; I, medial margin of pleopod 2 peduncle.

13.0), North Stradbroke Island, Moreton Bay, south-eastern Qld, 17 May 1985, on *Siganus spinus*, coll. Kui-po Leung (QM W13080). PARATYPES, 2 females (ovigerous about 12.0, non-ovigerous about 12.0, both without heads and first pereopods), male (6.0), same data as holotype (QM W13081). 3 females (ovigerous 10.5 dissected, non-ovigerous 10.0, 9.5), 7 males (5.0, 5.5, 6.0, 6.5, 8.0), locality as for holotype, 18 May 1985 (QM W13082).

**Type locality.** North Stradbroke Island, Queensland, Australia, about 27°26'S 153°25'E. (North Stradbroke is a large island of about 30 km; as no data was available as to the locality of collection it has been arbitrarily fixed here as the west coast between Dunwich and Amity Point).

**Description of female.** Body about 1.8 times as long as wide, dorsum weakly vaulted; widest at pereonite 5, twisted to one side. Cephalon anterior margin narrowed in front of eyes, forming broad subtruncate rostrum. Pereonite 1>2<3<4<5<6>7; pereonite 1 indented to receive cephalon, with 2 small lateral lobes behind eyes. Coxae of pereonites 2-4 inconspicuous or not visible in dorsal view; coxae of pereonite 6 as long as segment, coxae of pereonite 7 longer than segment. Coxae and pereonite lateral margins form an even outline. Pleon about 0.75 width of pereon, all pleonites visible; lateral margins of pleonite 1 concealed by pereonite 7; posterior pleonites very slightly narrower than anterior. Pleotelson narrowing from anterolateral margin, posterior margin broadly rounded.

Antennule extending to posterior of eyes; antenna

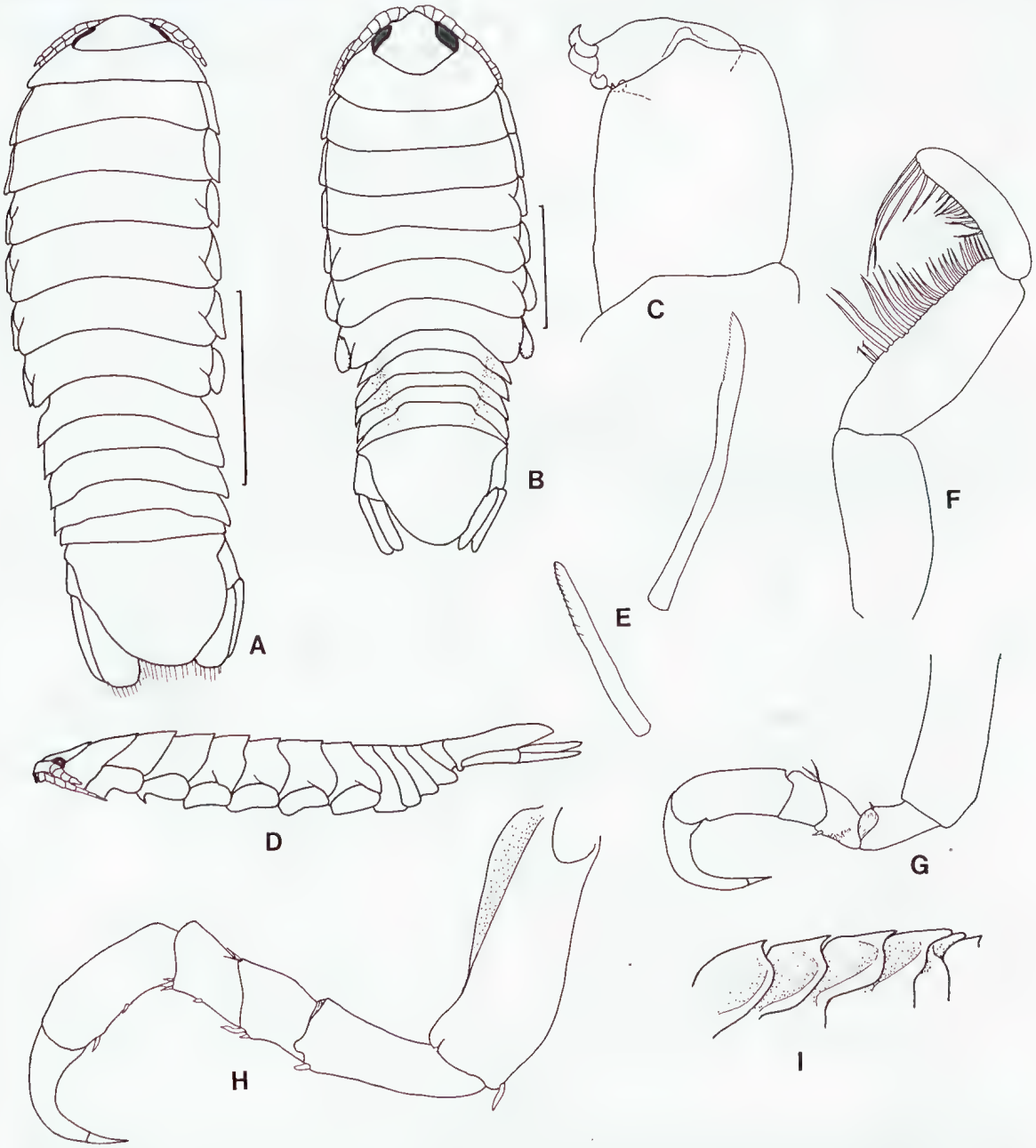


**Fig.15.** *Elthusa sacciger*. Figures of 17.0 mm except B and D. A, dorsal view; B, dorsal view, 21.5 mm; C, maxilliped articles 2 and 3; D, lateral view; E, spines from mandible palp article 3; F, mandible palp; G, pereopod 1; H, pereopod 7; I, left pleonites, ventral view. Scale lines represent 5.0 mm.

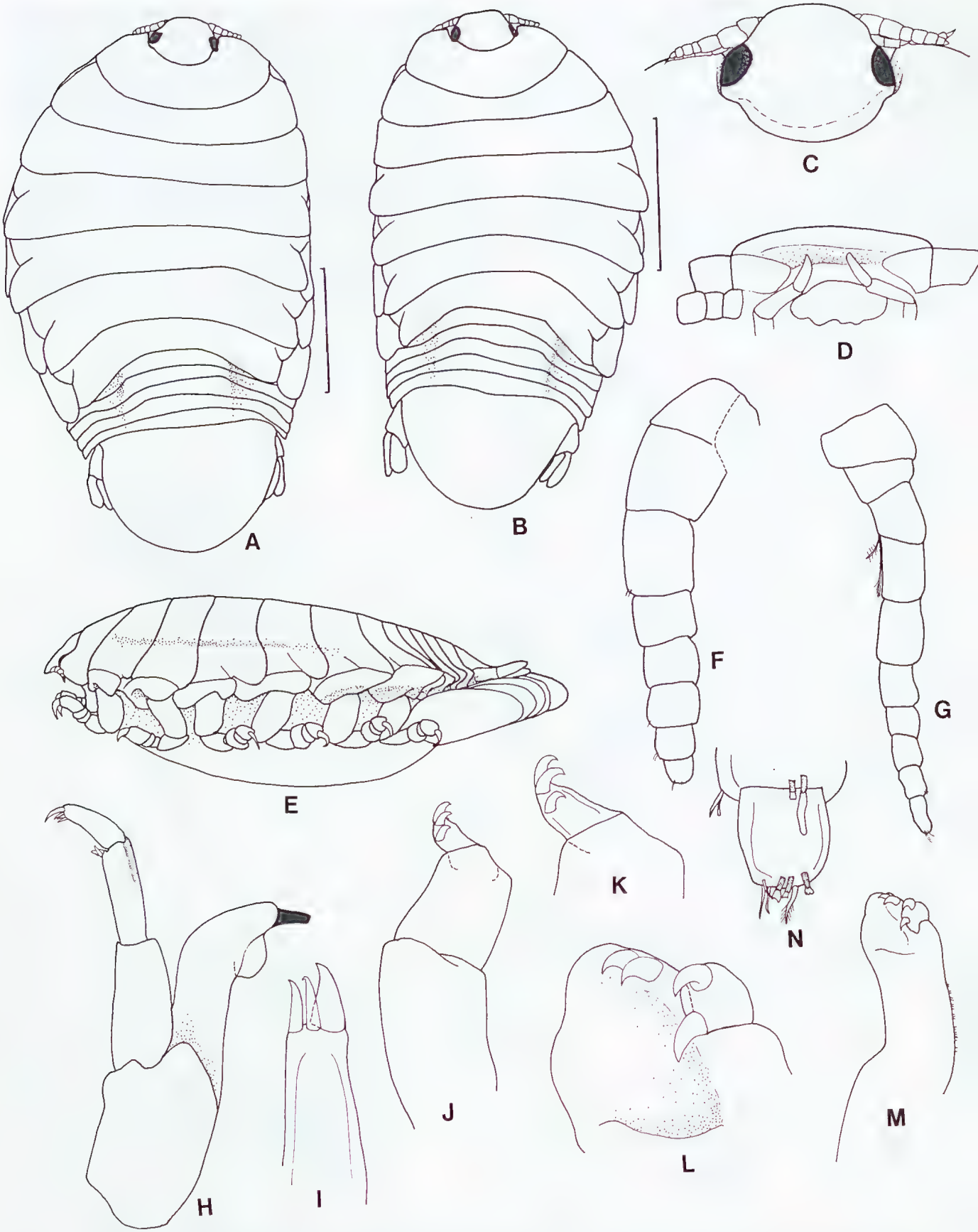


**Fig.16.** *Elthusa sigani* n.sp. A, C–E holotype, remainder female 10.5 mm (QM W13082) except B. A, dorsal view; B, dorsal view, 10.0 mm (QM 13082); C, cephalon; D, frons; E, lateral view; F, antennule; G, antenna; H, mandible; I, maxillule apex; J, maxilliped; K, maxilliped article 3; L, maxilla apex; M, maxilla; N, antennule, terminal article. Scale lines represent 3.0 mm.

longer, composed of 10 articles.

Mandible incisor robust, apex blunt; palp slender, article 1 longest; 2 spines at distolateral angle of article 2, 4 terminal spines on article 3. Maxillule with 2 slender and 1 broad based spine. Maxilla with 2 large curved spines each on medial and lateral lobe. Maxilliped without oostegital lobe; article 3 with 3 large recurved spines.

Pereopods 1-3 similar to each other. Pereopod 1 basis with feeble carina; merus posterior margin deeply cleft; dactylus slender, with anteroproximal depression. Pereopods 5-7 similar, except pereopod 7 only with distinct carina on basis; pereopod 7 merus deeply cleft, dactylus similar to that of pereopod 1. Brood pouch made up of pairs of alternately overlapping oostegites arising from sternites 2, 3, 4 and 5.

Pleopods 1 smaller than 2, pleopods 2, 3 and 4 approximately equal in size, pleopod 5 smaller than 4. Pleopod 2 with reduced appendix masculina arising in submedial position. Pleopods 3-5 endopod proximomedial lobe weakly developed. Peduncles to pleopods 1-4 with coupling hooks. Uropods short, reaching about half way along length of pleotelson, exopod slightly longer than endopod, both rami with broadly rounded apices.

**Male.** Body bilaterally symmetrical, about 2.0 as long as wide. Pleon about 0.80 width of pereon.

Appendages all similar to those of female but antennule and antenna slightly longer; mandible palp article 3 with slightly longer terminal setae. Pereopods with small spines on posterior margin of palm and carpus; carpus of pereopods 1-3 not deeply cleft; pleopod 2 appendix masculina longer than endopod, attached subbasally; uropods longer, extending to posterior of pleotelson. Paired penes present.

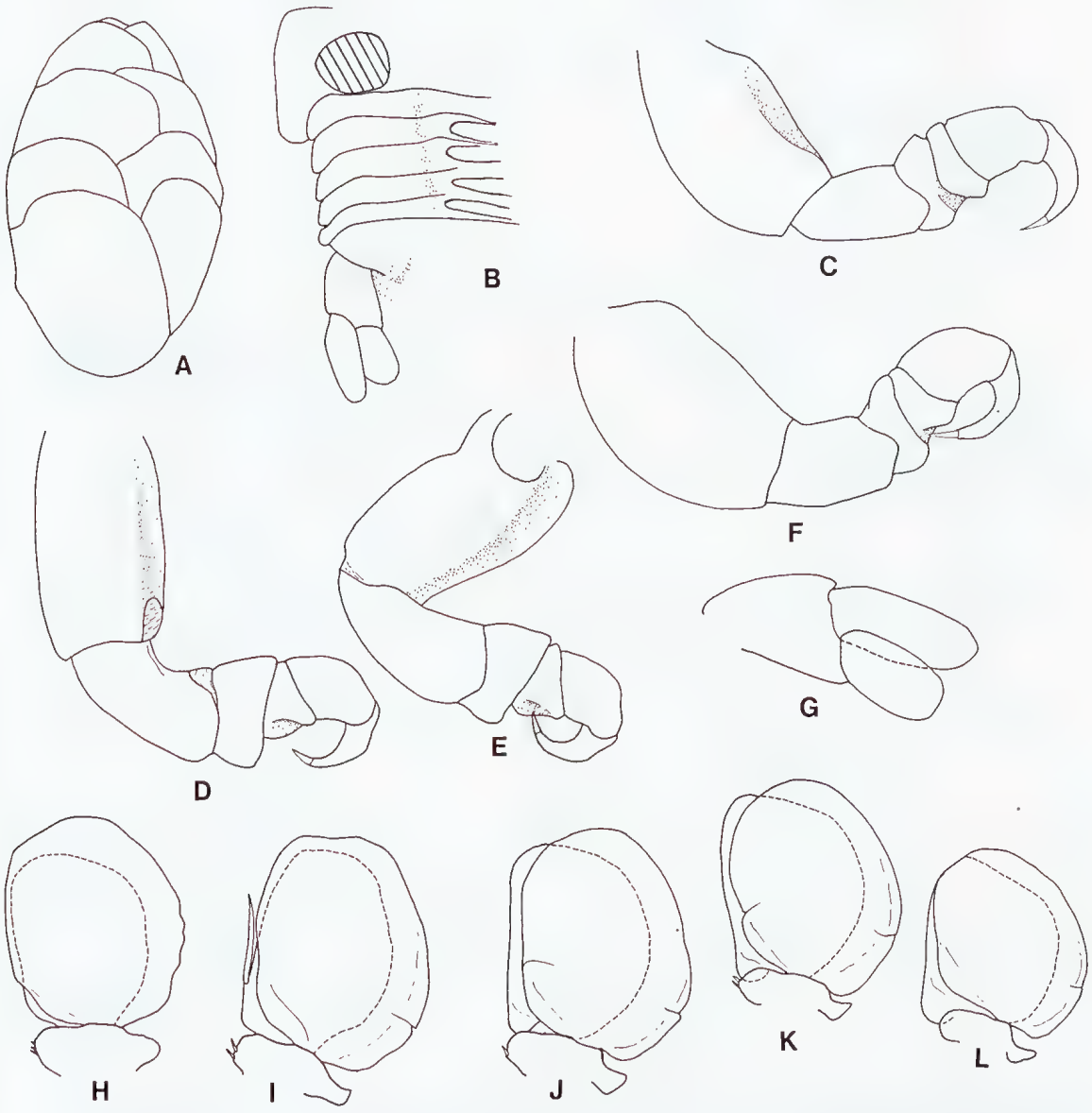


**Fig.17.** *Elthusa sigani* n.sp. All figs 10.5 mm (QM 13082). A, brood pouch; B, right pleonites, ventral view; C–F, pereopods 1, 2, 6, 7 respectively; G, uropod; H–L, pleopods 1-5 respectively.

**Colour.** White in alcohol, black chromatophores along lateral and posterolateral margin of pereonites and coxae, extending onto lateral margin of uropod peduncle and rami.

**Size.** Females to 13.0 mm, males between 5.0 and 8.0 mm.

**Variation.** Females may be twisted to left or to right, and coxae are longest on the most convex side.

**Remarks.** This small species is readily distinguished from all other Australian species of *Elthusa* by the even body outline, broad rostrum, antennules set wide apart, relatively long coxae and a wide pleon. The very much larger *Elthusa raynaudii* has similar coxal and pleonal morphology, but has a narrow rostrum, lacks the deeply cleft carpus on the pereopods and also has a distinct brood pouch and pleopod morphology.

The only similar Indo-Pacific species is the little

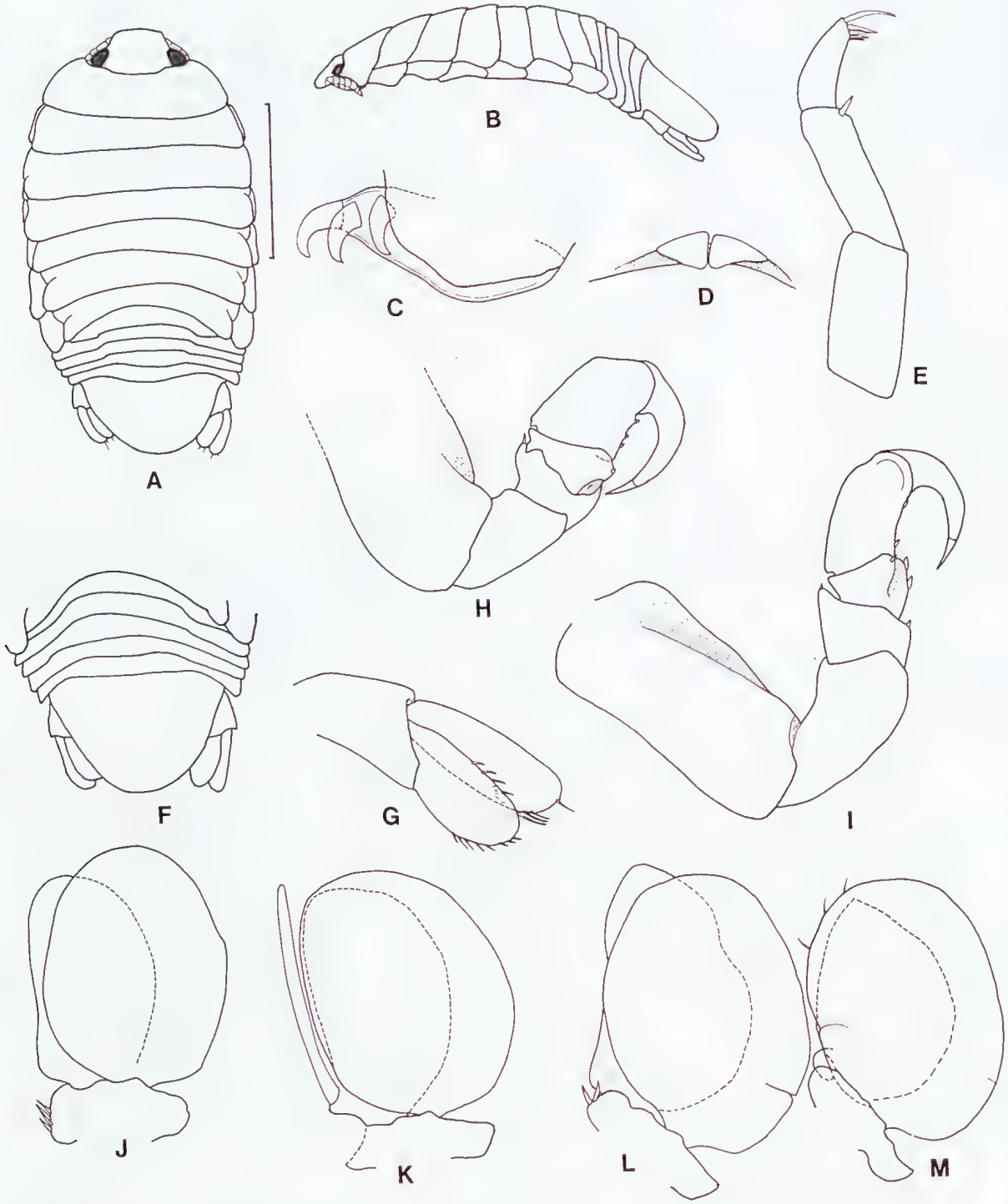


**Fig.18.** *Elthusa sigani* n.sp. All figs of male 5.5 mm (QM 13082). A, dorsal view; B, lateral view; C, maxilliped article 3; D, penes; E, mandible palp; F, pleon, perpendicular view; G, uropod; H, pereopod 1; I, pereopod 7; J–M, pleopods 1-3, 5 respectively. Scale line represents 2.0 mm.

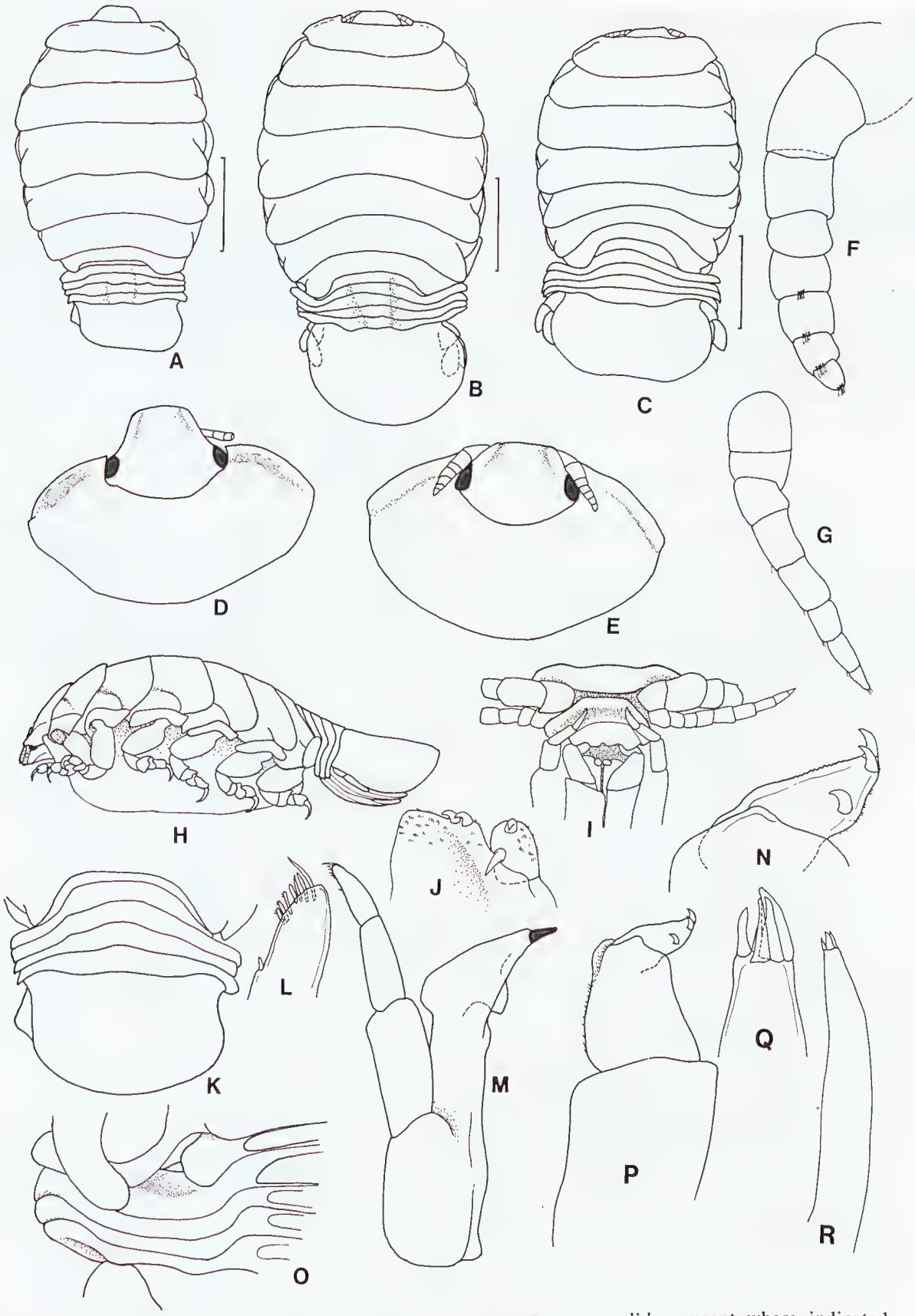


**Fig.19.** *Elthusa turgidula*. Figures of female 18.5, ex *Scarus sordidus* except where indicated. A, holotype, dorsal view; B, dorsal view; C, female 15.0 mm, ex *S. venosus*; D, cephalon, holotype; E, cephalon, ex *S. venosus*; F, antennule; G, antenna; H, lateral view; I, frons; J, maxilla apex; K, pleon and pleotelson, holotype; L, mandible palp article 3; M, mandible; N, maxilliped article 3; O, right pleonites, ventral view; P, maxilliped; Q, maxillule apex; R, maxillule. Scale lines represent 4.0 mm.

known *Elthusa emarginata*. This species is larger (21.5-27.0 mm) and has distinctive cephalic, pereopodal and coxal morphology.

**Distribution.** Known only from the type locality.

**Hosts.** *Siganus spinus* (F. Siganidae); position on the host was recorded only as on gills. Host specimens were not seen by the author.

**Etymology.** Epithet is derived from that of the host genus.

***Elthusa turgidula*** (Hale)

Figs 19–21

*Livoneca turgidula* Hale, 1926: 217, fig.11.–Nierstrasz, 1931: 144.

**Material examined.** Female HOLOTYPE (15.0), Fremantle, WA, 12 Sept. 1922, coll./don., G.E. Nicholls (WAM 10034). Male ALLOTYPE (9.5), Cottesloe, WA, Sept. 1924, coll./don. Glauert (WAM 11126). One Tree Island, Great Barrier Reef, 23°30'S 152°05'E: female (ovigerous 18.5), male (8.0), 20 Oct. 1967, gills of *Scarus*

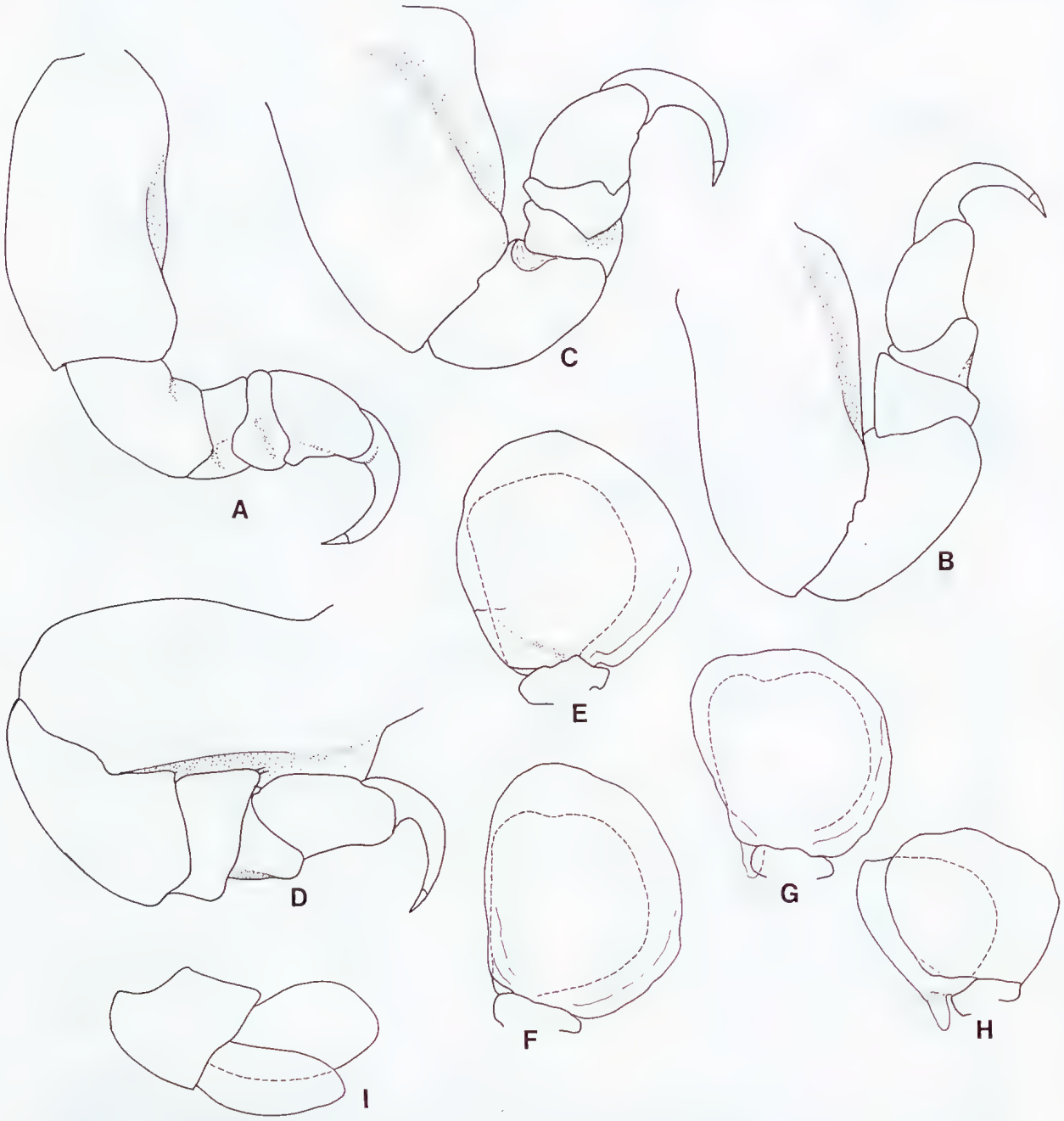


**Fig.20.** *Elthusa turgidula*. All figures from female 18.5 mm, ex *S. sordidus*. A–D, pereopods 1, 2, 6, 7 respectively; E–M, pleopods 1-3, 5 respectively; I, uropod.

*sordidus* (AM I15634-023) depth 2 m, coll. F. Talbot and party (AM P37781). Female (non-ovigerous 15.0), 2 Dec. 1966, gills of *Scarus venosus* (AM I15623-28), coll. Talbot (AM P37782). Male (12.5), 19 Sept. 1968, gills of *Scarus* sp. (AM I17445-137), coll. H.K. Larson (AM P37783).

**Type locality.** Fremantle, Western Australia.

**Description of female.** Body 1.7 times as long as wide, dorsum moderately vaulted; anteroposteriorly arched; widest at pereonite 3 or 4. Cephalon deeply immersed in pereonite 7; anterior margin weakly to moderately produced; anterolateral margins with indistinct ridge; eyes small, 0.23 width of cephalon. Pereonite 1>2<3<4>5>6>7. Pereonite 1 with sublateral depression. Coxae not conspicuous in dorsal view. Pereonite 7 posterior margin deeply indented. Pleon 0.31 (holotype to 0.52) width of pereon; pleonite 1 less than half as wide as pleonite 2; pleonites 2-5 about equal in width. Pleotelson broadly and smoothly rounded, about 1.0-0.66 as wide as long.

Antennule extending to posterior of eye, robust; antenna shorter and more slender than antennule, composed of 8 articles; bases of both widely separated.

Mandible palp slender, article 3 with 7 stout distomedial setae. Maxillule with 5 terminal spines. Maxilla distally wide; 2 hooked spines each on medial and lateral lobes. Maxilliped without laminar lobes; article 3 with 3 recurved spines.

Pereopods 1-4 slightly shorter than 5-7. Pereopod 1 basis with outer lateral carina; pereopods 2-7 basis with carina. Pereopods 5-7 carpus with grooved posterior margin.

Pleopods with all rami lamellar; peduncles without accessory lamellae; endopods of pleopods 3-5 with simple proximomedial lobe. Pleopods 1-5 progressively decreasing in size. Uropods short, about half length of pleotelson; exopod shorter than endopod, apex acute; endopod apex broadly rounded.

**Male.** Generally similar to female but for: body margins subparallel and coxae more conspicuous in dorsal view; triangular penes present on sternite 7; pleopod 2 endopod with prominent appendix masculina; uropods with both rami broadly rounded; mandible palp article 3 with longer setae.

**Colour.** Pale tan in alcohol.

**Size.** Females 15.0-18.5 mm, males 8.0-12.5 mm.

**Variation.** The holotype has the anterior margin of the cephalon more strongly produced than the One Tree Island specimens. Relative width of the pleon from 0.31-0.52 width of pereonite 4. The pleotelson has the posterior margin evenly rounded or slightly flattened.

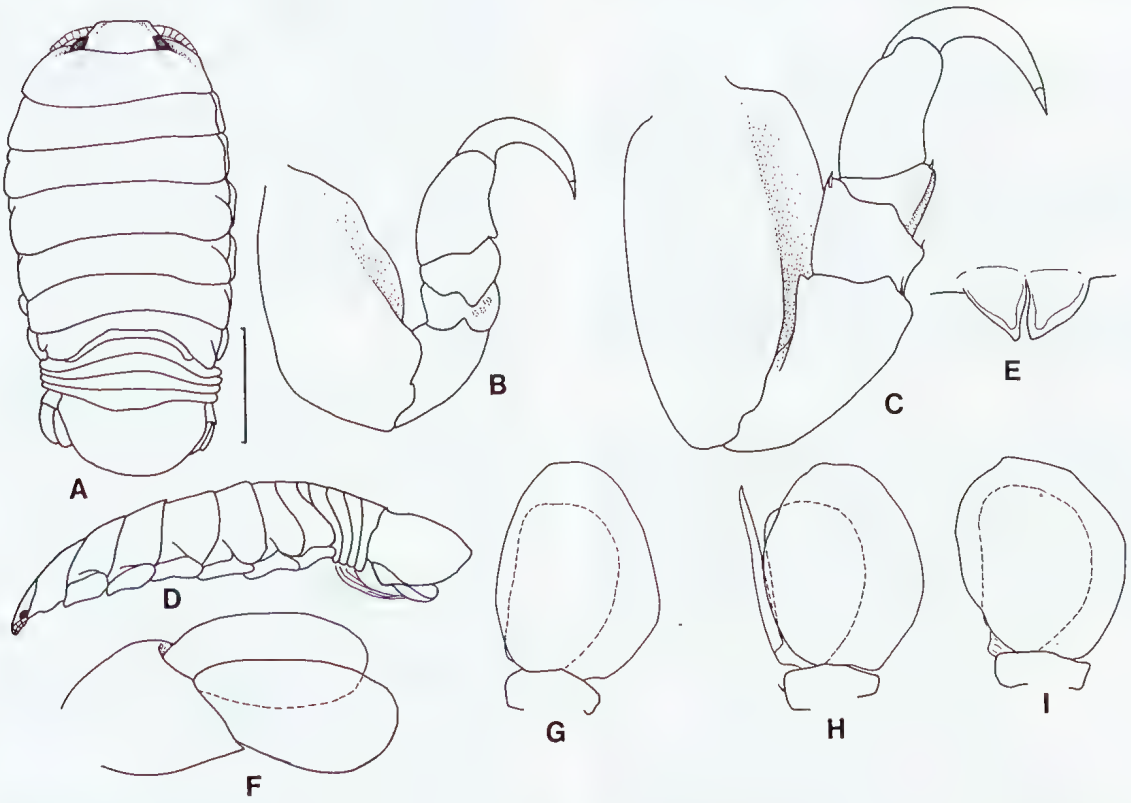


**Fig.21.** *Elthusa turgidula*. All figures of male, ex *S. sordidus*. A, dorsal view; B, pereopod 1; C, pereopod 7; D, lateral view; E, penes; F, uropod; G–I, pleopods 1-3 respectively. Scale line represents 2.0 mm.

The cephalon is angled down in all specimens except the holotype and allotype.

**Remarks.** The very narrow first pleonite, wide anterior margin to the cephalon with anterolateral ridges and widely separated antennule bases separates this species from all others of the genus.

**Hosts.** *Scarus sordidus*, *Scarus venosus* and an unidentified *Scarus* sp., all at One Tree Island. The female isopod attaches about half way along a gill arch, with the abdomen facing laterally to the host ("outwards"), and the head projecting into the buccal spaces of the host.

**Distribution.** Cottesloe and Fremantle, WA; One Tree Island, southern Great Barrier Reef.

### *Ichthyoxenus* Herklots

*Ichthyoxenus* Herklots, 1870: 128.–Schiödte & Meinert, 1884: 297.–Richardson, 1913: 559.–Shen, 1936: 5.–Brian & Darteville, 1949: 132.–Lincoln, 1972: 329.–Kussakin, 1979: 291.

**Type species.** *Ichthyoxenus jellinghausi* Herklots, 1870, by monotypy. The types (3 females, 1 male) are held at the Rijksmuseum van Natuurlijke Historie, Leiden. New material of this species is needed before it can be redescribed.

**Provisional diagnosis.** Body vaulted; strongly ovate, nearly circular in dorsal view; bilaterally symmetrical. Cephalon not deeply immersed in pereonite 1. Coxa all short, rounded. Pleon narrow (less than 0.5 pereon), pleonite 1 partly overlapped by pereonite 7.

Antennule shorter than antenna, bases set apart. Pereopods with distal articles (ischium to carpus) flattened, widest distally; dactylus short, flattened (not rounded in section as in other genera). Pleopods (of type species) not known.

**Composition.** Other than the type species, it is at present uncertain how many described species should be placed in this genus. On the basis of the provisional diagnosis above, or recorded habitat, I include the following: *Ichthyoxenus africana* (Lincoln, 1972), n.comb., *Ichthyoxenus amurensis* (Gersfeldt, 1858), *Ichthyoxenus expansus* Van Name, 1920, *Ichthyoxenus formosanus* Harada, 1930, *Ichthyoxenus geei* Boone, 1921, *Ichthyoxenus japonensis* Richardson, 1913, *Ichthyoxenus montanus* Schiödte & Meinert, 1884, *Ichthyoxenus sinensis* Shen, 1936, *Ichthyoxenus tanganyikae* (Fryer, 1965). To this list of freshwater species I add the marine species *Ichthyoxenus micronyx* (Miers, 1880) n.comb., *Ichthyoxenus minabensis* (Shiino, 1956) n.comb. and *Ichthyoxenus puhi* (Bowman, 1962), n.comb.

**Remarks.** The status of the genus *Ichthyoxenus* has long been questioned, first by Miers (1880), then Gerstaecker (1882), followed by Monod (1931), Brian & Dartevelle (1949), and in more detail by Fryer (1965) and Lincoln (1972). The two central themes to the argument of these authors was the supposed synonymy of *Ichthyoxenus* to *Livoneca* (Miers, 1880; Gerstaecker, 1882; Monod, 1931; Brian & Dartevelle, 1949) and the supposed polyphyletic origin of *Ichthyoxenus* (Fryer, 1965; Lincoln, 1972). The emphasis of all authors was that the habitat could not be used to discriminate genera, that the "genus" arose independently on several occasions and that *Ichthyoxenus* was undoubtedly a synonym of *Livoneca*.

Brusca (1981:131) contributed to the discussion by suggesting that *Ichthyoxenus* should be used for all Asiatic freshwater flesh burrowers, with the implication that species in such different habitats (gill/buccal attaching versus flesh burrowing) warrant separate genera. The logic of this is no different to that of separating genera by marine versus freshwater.

An important aspect of this discussion is that no authors redescribed or redefined the genera concerned and their opinions were based only on the literature and on species they had at hand, which in some cases were none. Morphological criteria were often not considered, or considered and then discounted such as in Brusca's (1981) assertion that the two genera could not be distinguished by morphological criteria. The type species of both *Livoneca* and *Ichthyoxenus* were at that time effectively undescribed.

It is now apparent that two genera have little in common, are belong to separate subfamilies. Previous considerations of their status, based on a misconception of *Livoneca*, are invalid. Undoubtedly the genus *Ichthyoxenus* needs a full revision, and a full redescription of the type species. It is also certain that several species of freshwater cymothoids do not belong in *Ichthyoxenus*, but until they are described in full, their true generic position remains uncertain. An annotated list of all freshwater "*Livoneca*" and *Ichthyoxenus* is here provided.

The majority of species are from China and the Far East. The status of many species is open to question (Harada, 1936; Trilles, 1976), and all are in need of redescription. *Ichthyoxenus micronyx* lacks detailed habitat data and it is not known if it does burrow into host flesh.

*Ichthyoxenus minabensis* and *I. puhi* are not flesh burrowers, and also are rather narrower than others of the genus. These species have the characteristic pereopod morphology, and for this reason are placed in the genus. At present there are no morphological criteria to separate gill attaching from buccal attaching species (e.g. *I. expansus*, *I. tanganyikae*) from flesh burrowing species (e.g. *I. jellinghausi*, *I. sinensis*).

In common with several cymothoid genera and species, the generic spelling used has varied. Van Name (1920) and Brusca (1981) used *Ichthyoxenos*; Dartevelle (1939) used *Ichtyoxenus*.

### Freshwater Species Previously Placed in *Livoneca* and *Ichthyoxenus*.

1. *Livoneca africana* Lincoln, 1972. Lake Tanganyika, Tanzania. From the mouth of two species of cichlid fishes. Here transfered to *Ichthyoxenus*.
2. *Ichthyoxenus amurensis* (Gersfeldt, 1858). Figured by Kussakin (1979).
3. *Livoneca daurica* Miers, 1877. Junior synonym of *Ichthyoxenus amurensis* (Kussakin, 1979).
4. *Livoneca enigmatica* Fryer, 1968. Taken from the body surfaces and gill cavity of two species of clupeid fishes. I am uncertain of the correct generic position.
5. *Ichthyoxenus expansus* Van Name, 1920. Holotype taken from gills of a characinid fish, Uele River, Zaire.
6. *Ichthyoxenus formosanus* Harada, 1930. Taiwan.
7. *Ichthyoxenus geei* Boone, 1921. Soochow, China (Shen, 1936). From external surface of hosts.
8. *Ichthyoxenus japonensis* Richardson, 1913. Lake Biwa and at Omi on Lake Yogo, Japan.
9. *Ichthyoxenus jellinghausi* Herklots, 1870. Type species for the genus. Additional figures given by Richardson (1913).
10. *Livoneca guianensis* Van Name, 1925. Katarbo, British Guiana. From gills of river fishes (Van Name, 1936). I am uncertain of the correct generic position, it does not agree with the diagnosis for *Ichthyoxenus*.
11. *Livoneca lazzari* (Pearse, 1921). Van Name (1936) repeats the description. The species is based on immature material, and I am uncertain of the correct generic position.
12. *Ichthyoxenus montanus* Schiödte & Meinert, 1884. Himalayas.
13. *Ichthyoxenus opisthopterygium* Ishii, 1916. Lake Biwa, Japan.
14. *Livoneca orinoco* Bowman & Ungria, 1957. This species does not belong to *Ichthyoxenus*.
15. *Livoneca parasilura* Shen, 1936. Peiping, Hopei Province, China. Differs markedly from other freshwater species, and appears most similar to *Livoneca sensu strictu*.
16. *Ichthyoxenus sinensis* Shen, 1936. Peiping, Hopei Province, China. Parasitic in the body.
17. *Livoneca symmetrica* Van Name, 1925. Katarbo, British Guiana, on several species of river fishes (Van Name, 1936). I am uncertain of the correct generic position, but it is not an *Ichthyoxenus*.
18. *Livoneca tanganyikae* Fryer, 1965. Recorded from mouth, on one species of host only. Lake Tanganyika, Tanzania.
19. *Ichthyoxenus tchangi* Yü, 1935. Yunnan, China.

### *Ichthyoxenus minabensis* (Shiino)

Figs 22, 23

*Indusa minabensis* Shiino, 1951: 83, fig.3.

**Material examined.** Female (non-ovigerous 17.0), Marian Plateau, 22°34.8'S 153°38.7'E, 16 Nov. 1985, on *Chaunax fimbriata*, 316 m depth, coll. A.J. Bruce on FRV *Soela* (NTM Cr6699).

**Types.** Deposition of the type specimens was not indicated by Shiino (1955).

**Type locality.** Off Minabe, Wakayama Prefecture, 182-366 m.

**Description.** Body strongly vaulted, symmetrical, about 1.9 times as long as wide. Cephalon anterolateral margin straight, converging to apical point, apex of which is turned down; eyes about 0.3 width of cephalon. Pereonite 1 distinctly narrower than pereonite 2; pereonites 2-5 with lateral margins thickened; posterolateral margins of pereonites 2-7 produced, rounded. Pereonites 1<2<3>4<5>6>7; pereonite 5 widest. Coxae all shorter than respective segment; anterior margin of coxae 5-7 concealed by preceding segment. Pleonite 1 lateral margins overlapped by posterolateral margins of pereonite 7; pleonites subequal in width, about 0.3 width of pereonite 5. Pleotelson as long as wide, posterior margin broadly rounded.

Antennule bases close set but not contiguous; composed of 8 articles, extending beyond posterior of eye. Antenna bases set wide apart; composed of 11 articles, extending to pereonite 1.

Mandible palp article 3 with about 6 short setae. Maxillule with 4 terminal spines. Maxilla with 2 spines each on medial and lateral lobes. Maxilliped article 3 with 3 recurved terminal spines.

Pereopods 1-3 manifestly shorter than 5-7. All pereopods without carina on bases, and all with short flat sided dactylus. Pereopod 1 merus dilated. Pereopod 7 merus and carpus somewhat flattened and expanded (1.4 and 1.7 times as wide as long respectively).

Pleopods all lamellar, peduncles and rami without lamellar lobes; proximomedial lobe of endopods 3-5 weakly developed. Pleopod 1 largest, 5 smallest. All exopods with dense distomedial patch. Uropods short, extending about half way along pleotelson, both rami bluntly rounded; exopod slightly longer than endopod.

**Colour.** Pale brown in alcohol, eyes black.

**Remarks.** This specimen agrees entirely with the English description and figures given by Shiino (1951), and is also recorded from the same host species.

The most similar species to *I. minabensis* is *I. puhi* (Bowman). The distinctive pereonite morphology is shared by both species, and *I. minabensis* differs from

*I. puhi* by having the cephalon anterior margin narrow, narrower pleon, wider uropod rami, and the uropod endopod shorter than the exopod (in *I. puhi* the endopod is longest). Both species are from sedentary, bottom-dwelling hosts.

Miers (1880) described a similar species, *Livoneca micronyx* from Mauritius. Examination of the type specimen shows that this species differs in having the merus of pereopods 6 and 7 more distinctly lobed, lateral margin of the pereonites not thickened, and the

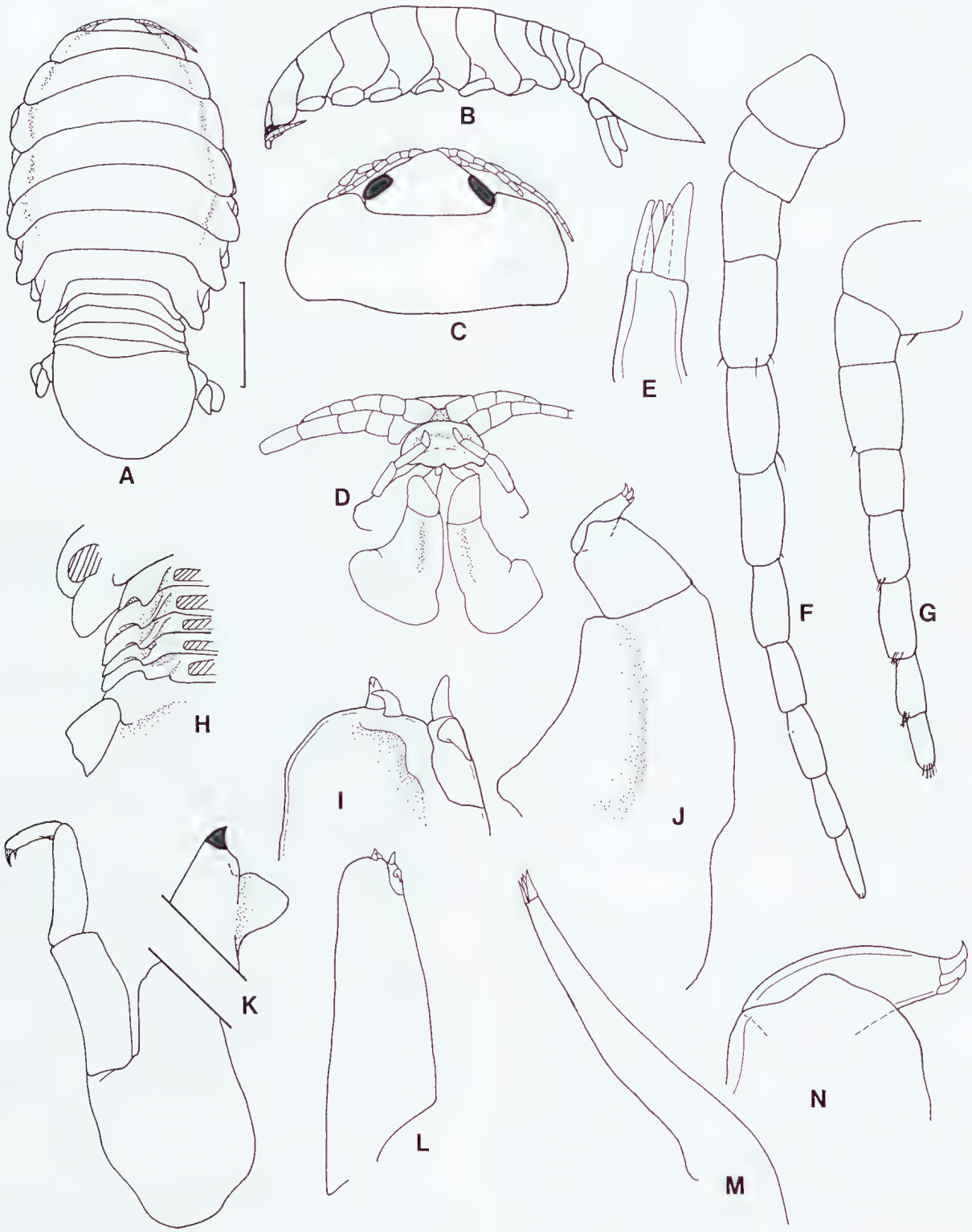


**Fig.22.** *Ichthyoxenus minabensis*. Figs all NTM Cr6699. A, dorsal view; B, lateral view; C, head, pereonite 1; D, frons; E, maxillule apex; F, antenna; G, antennule; H, right pleonites, ventral view; I, maxilla apex; J, maxilliped; K, mandible (broken); L, maxilla; M, maxillule; N, maxilliped article 3. Scale line represents 4.0 mm.

pleonites overlapping one another laterally.

**Hosts.** Recorded from the mouth of *Chaunax fimbriatus* by Shiino (1955), the position of the present material was not recorded.

**Distribution.** One previous record from Japan, here recorded from north-eastern Australia.

### *Idusa* Schiödte & Meinert

*Idusa* Schiödte & Meinert, 1884: 334.–Trilles, 1981: 593 [not *Indusa* (*lapsus*)].–Richardson, 1905: 246 [not *Idusa*].–Brusca, 1981: 190.

**Type species.** *Idusa plagusiae* Schiödte & Meinert, 1884; held at the Zoologisk Museum, Copenhagen.

**Provisional diagnosis of female.** Body twisted to one side; dorsum moderately vaulted. Cephalon moderately immersed in pereonite 1, posterior margin not trilobed. Coxae all small, all shorter than respective segment. Pleon not immersed in pereon; pleonite 1 manifestly narrower than 2; pleonites 2-5 subequal in width.

Antennule shorter than antenna; both antennule and antenna slender; bases set very close. Mouthparts not known. Pereopods slender, basis without carina, dactylus large. Pleopods with rami all lamellar; without accessory lobes; peduncles without accessory lobes.

**Composition.** Only one other species: *Idusa dieuzeidei* Dollfus, 1950 (see Trilles, 1976b).

**Remarks.** This is yet another genus in which species have been placed, and diagnosed with only limited knowledge of the morphology of the type species.

It is clear that Richardson's (1905) diagnosis was based on *Idusa carinata*. Brusca's (1981) diagnosis, largely the same as Richardson's (1905) diagnosis, is also obviously based on *I. carinata*. Trilles (1981) indicated that of the species then placed in *Idusa* (again misspelt by several authors as *Indusa*) other than the type species, only *I. dieuzeidei* could be considered to belong to the genus. The other species were *I. carinata* Richardson, *I. ophueseni* Pillai, 1954, *I. pustulosa* Pillai, 1954 and *I. malayi* (Tiwari, 1953). Of these, *I. malayi* has been placed back into *Agarna* by Bowman & Tareen, 1983 and *I. ophueseni* is a synonym of *Agarna malayi* (see Pillai, 1964).

*Idusa pustulosa* differs little from *Agarna malayi* (see Pillai, 1964) and should be transfered to *Agarna*. *Idusa carinata* will at present have to be retained in the present combination as *incerta sedis*. While agreeing with *Idusa* in the antennules being close set, small compact coxae, and narrow pleon, it differs in having an ovate and symmetrical body, cephalon deeply immersed in pereonite 7, pleonite 1 not markedly narrower than 2, more robust antenna and robust pereopods, the bases which are carinate.

There are at present no species of this genus recorded from Australia. The rediagnosis of this genus was necessary to allow for positive generic location of

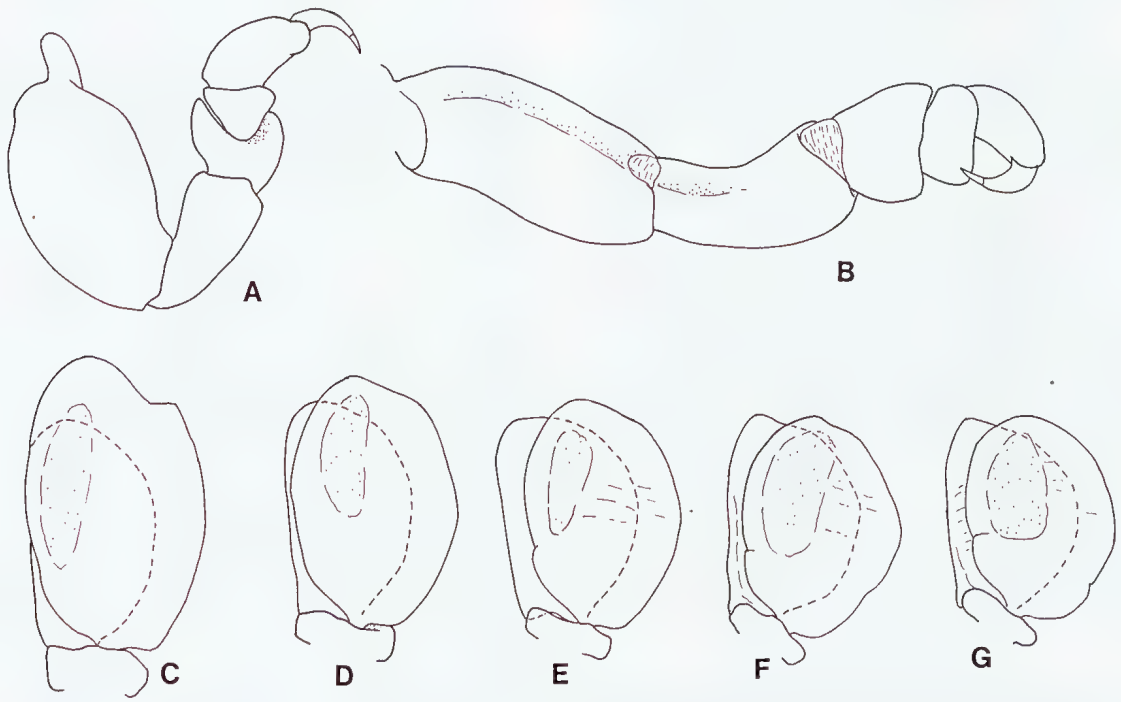


**Fig.23.** *Ichthyoxenus minabensis*. All figs NTM Cr6699. A, pereopod 1; B, pereopod 7; C–G, pleopods 1-5 respectively.

*Catoessa ambassae*, which is in many ways similar to *Idusa plagusiae*, an Indian Ocean species (Schiödte & Meinert, 1884).

The diagnosis given here is provisional as fresh material of the type species is needed before a full description can be provided.

## **Anilocrinae** Schiödte & Meinert

**Remarks.** Bruce (1987c) rediagnosed the subfamily Anilocrinae and provided a key to the then known Indo-West Pacific genera. That key now applies only those genera attaching externally on the host. Two further genera are here added to the Indo-West Pacific representatives of the subfamily: *Enispa* Schiödte & Meinert and *Norileca* n.gen. The transfering of *Livoneca* into the Anilocrinae in effect also synonymises Livonecinae with Anilocrinae.

## *Enispa* Schiödte & Meinert

*Enispa* Schiödte & Meinert, 1884: 292.

**Type species.** *Cymothoa irregularis* Bleeker, 1857 by monotypy. Two ovigerous female syntypes (collected by Bleeker) are held at the Rijksmuseum van Natuurlijke Historie, Leiden (RMNH 62).

**Diagnosis of female.** Body strongly vaulted, about 3 times as long as wide. Cephalon moderately immersed in pereonite 1, posterior margin weakly trilobed. Coxae of pereonites 2-4 as long as respective segment; coxae of pereonites 5-7 longer than respective segment. Pleon not immersed in pereon, all segments visible in dorsal view; lateral margins ventrally directed. Pleotelson cupola shaped, vaulted.

Antennule shorter than antenna, bases set wide apart.

Pereopods without basal carina, articles not dilated. Brood pouch arising from sternites 1-4, and 6, with posterior pocket; oostegites of sternite 6 posteriorly produced and extending over pleopods. Pleopods with laminar lobes on lateral margin of peduncle and proximomedial angle of endopods 1 and 2; pleopods 3-5 with folded proximomedial lobe; endopods of pleopods 3-4 with single large fold, endopod of pleopod 5 with 2 large complexly folded lobes, distal margin indented.

**Composition.** *Enispa convexa* (Richardson, 1905), n.comb. The figures given by Brusca (1981) allow this species to be confidently placed in this genus (see the *Livoneca* species list for comments of *E. convexa*).

**Remarks.** This is yet another small genus of Schiödte & Meinert's that has long been ignored. The type species was until now effectively undescribed, and consequently the genus itself undefined by contemporary standards. It can be distinguished from all other anilocrine genera by the strongly vaulted body shape and the rounded pleotelson. Typically the uropods are held concealed under the pleotelson, and are not visible in dorsal view.

The morphology of the brood pouch and pleopods places this genus within the Anilocrinae as redefined by Bruce (1987c). The pleopods are nearly identical to those of *Nerocila*.

### *Enispa irregularis* (Bleeker)

Figs 24, 25

*Cymothoa irregularis* Bleeker, 1857: 34, pl.2, fig.11.–Gerstaecker, 1882: 261.

*Cymothoa paradoxa* Haller, 1880: 378, pl.18, figs 5-7.–Gerstaecker, 1882: 261.

*Enispa irregularis*.–Schiödte & Meinert, 1884: 293, pl.11, figs 1-4.–Nierstrasz, 1915: 95.–Nierstrasz, 1931: 137.–Trilles, 1979: 259, pl.1, fig.6.

**Material examined.** 2 females (ovigerous 19.0, 23.0, SYNTYPES), Oost Indie, coll. P. Bleeker (RMNH 62). Female (ovigerous 17.0, holotype of *C. paradoxa*), dans la bouche d'une *Caranx carangus* Bloch, (locality illegible: ?Madagascar), trouvé par G. Lunel (MHNG 14). Female (ovigerous 13.5), Jan. 1910, and female (ovigerous 15.5), Aug. 1910, both Baai v Batavia (= Jakarta, Java, Indonesia), coll. P.J. Buitendijk (RMNH 61). Female (non-ovigerous 15.0), Arafura Sea, 12°18'S 127°27'E, 25 Sept. 1984, from stomach of trawled dolphin, coll. D. Hembrost (NTM Cr6563).

**Type locality.** Amboina, Indonesia (Bleeker, 1857).

**Description of female.** Body strongly vaulted, about 2.3 times as long as wide; lateral margins subparallel. Cephalon moderately immersed in pereonite 1, posterior margin trilobed; eyes indistinct. Pereonite 1 with anterolateral margin produced, about half way along cephalon; pereonite 1 longest, 2 and 7 shortest; pereonite 1>2<3=4=5<6>7. Pleon about one third as wide as pereon, lateral margins of all pleonites arching posteriorly. Pleotelson subquadrate in dorsal view.

Antennule with 8 articles, antenna with 11 articles; articles 1 and 2 of both appearing partially coalesced. Mandible palp article shortest; article 3 very slightly longer than 2, markedly flattened. Maxillule with 1 large and 3 slender terminal spines. Maxilla with 2 small spines each on medial and lateral lobe. Maxilliped article 3 with 2 terminal recurved spines.

Pereopod 1 robust; dactylus large, extending to merus; basis with weak carina. Pereopods 2 and 3 similar to 1. Pereopods 5-7 longer than 1-3; basis with more prominent carina; dactylus extending to posterior of carpus. Brood pouch with posterior oostegites extending over pleopods.

Pleopods as for generic diagnosis. Uropod rami shorter than peduncle; endopod slightly longer than exopod, both rami bluntly rounded.

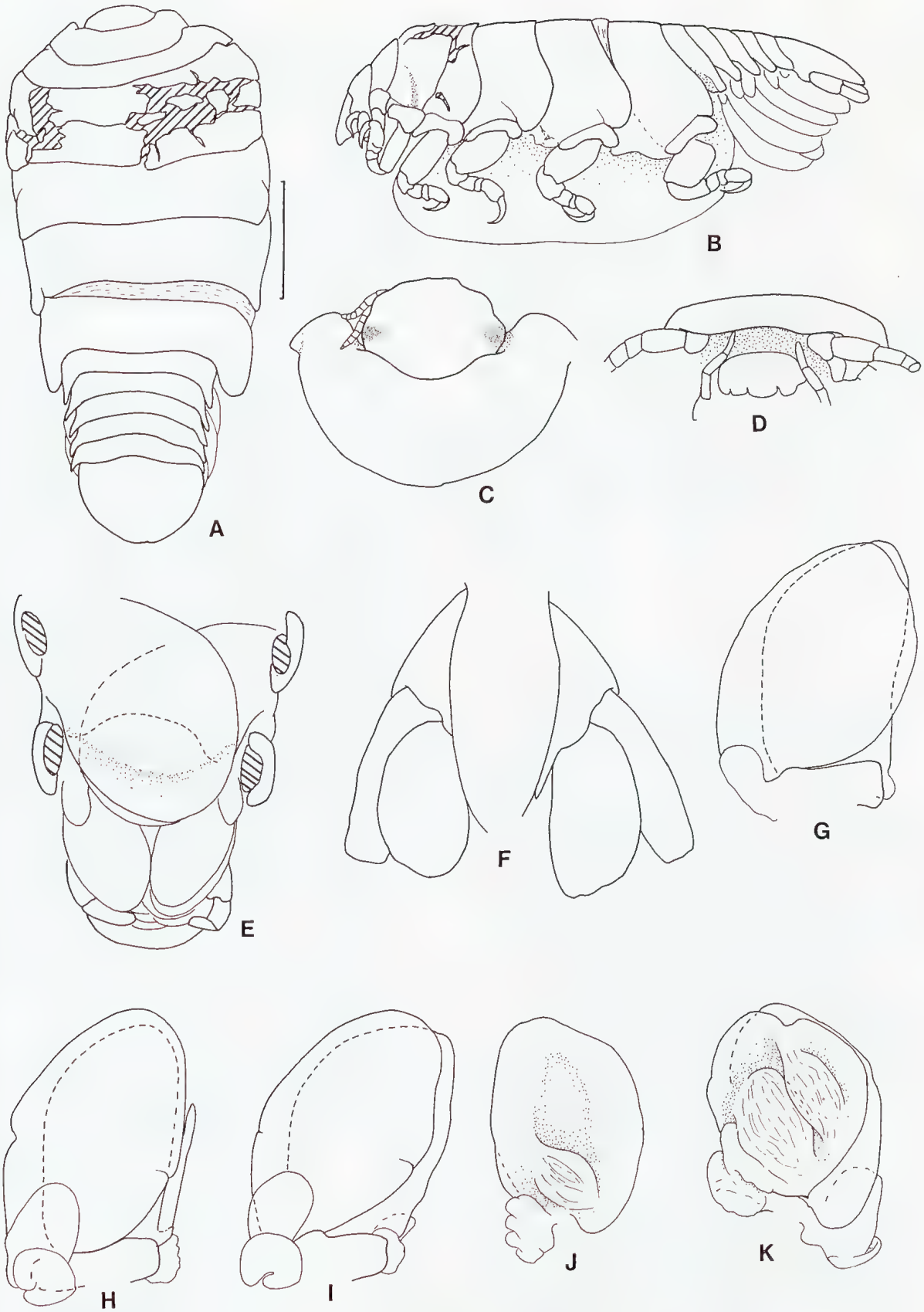


**Fig.24.** *Enispa irregularis*. A–C, F, 23.0 mm syntype; G–K, female 15.5 mm RMNH 61; remainder as indicated. A, dorsal view; B, lateral view; C, cephalon, pereonite 1; D, frons 19.0 mm syntype; E, posterior of brood pouch, 13.5 mm syntype; F, left and right uropods, *in situ*; G–I, pleopods 1-3 respectively; J, pleopod 3 endopod, dorsal side; K, pleopod 5 endopod dorsal view. Scale line represents 5.0 mm.

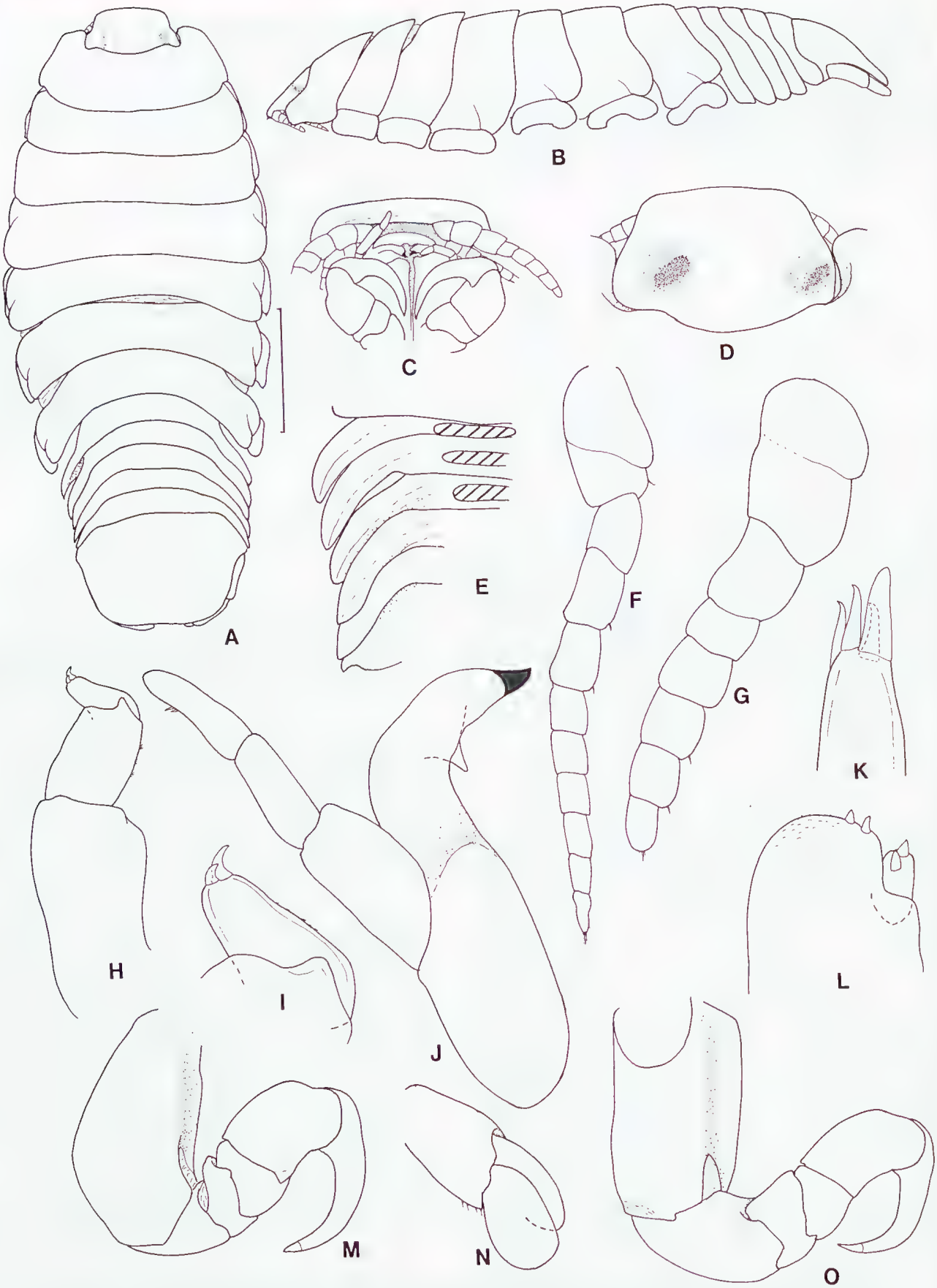


**Fig.25.** *Enispa irregularis*. All figs of NTM Cr6563. A, dorsal view; B, lateral view; C, frons; D, cephalon; E, right pleonites, ventral view; F, antenna; G, antennule; H, maxilliped; I, maxilliped article 3; J, mandible; K, maxillule apex; L, maxilla apex; M, pereopod 1; N, uropod; O, pereopod 7. Scale line represents 3.0 mm.

**Male.** Not known.

**Colour.** Pale tan in the Northern Territory specimen, no chromatophores apparent.

**Size.** 13.5-23.0 mm.

**Variation.** The largest syntype has the uropod rami subequal in length, with the exopod apex subtruncate and the posterior margin of the pleotelson rounded rather than subquadrate. With the limited material at hand it is not possible to assess intraspecific variation for this species.

**Remarks.** This species has been rarely recorded since first described; the only illustrations are of whole animals. Superficially this does look like a species of *Cymothoa*, but the pleon, pereopod and pleopod morphology clearly separates it from that genus.

The figures given by Menzies *et al.* (1955) of *Livoneca convexa* appear identical to the material at hand of *E. irregularis*, the only difference being in the spination of the maxilla of ovigerous females. In particular the uropods of the present material agrees with that figured by Menzies *et al.* (1955) rather than that figured by Brusca (1981). Brusca's (1981) material also differs in having the pleotelson posterior margin more narrowly rounded. From his remarks it is apparent that Brusca examined material from two species of Carangidae. Brusca designated a neotype and neoallotype from a very different host (Serranidae, *Serranus* sp.) to that recorded by Menzies *et al.* (Carangidae, *Chloroscombrus orqueta*) and from a very different habitat (demersal compared to pelagic). In view of the morphological differences the conspecificity of material from *Serranus* with that from *Chloroscombrus* must be questioned. Similarly, the status of *E. convexa* (*sensu* Menzies *et al.* 1955, on *Chloroscombrus*) in relation to *E. irregularis* also needs further examination.

**Hosts.** Haller (1880) recorded the species from *Caranx carangus* Bloch. No other host records exists.

**Distribution.** Reliable records are from Indonesia, Amboina and Australia. I cannot determine where Haller's (1880) material originated. The label is not clearly legible, and has a name that could equally be Madagascar or Macassar. Haller (1880) stated the locality as the Indian Ocean.

### *Livoneca* Leach

*Livoneca* Leach, 1818: 351. Not *Livoneca* or *Lironeca* of all other authors.

**Type species.** *Livoneca redmanii* Leach, 1818. The holotype is held at the British Museum (Natural History), London (BMNH 1979: 401.1).

**Diagnosis of female.** Body weakly vaulted, twisted to one side. Cephalon anterior margin folded back, but not projecting between antennal bases. Posterior margin trilobed. Coxal plates as long or longer than respective segment. Pleon not immersed in pereon, pleonites becoming progressively narrower towards posterior; ventrolateral margin of pleonites 1 and 2 or 1-3 weakly bilobed.

Antenna longer than antennule, bases set wide apart, not dilated or flattened. Mandible palp articles slender, not flattened or expanded.

Pereopods robust, all with large dactylus, without expanded carina on basis. Brood pouch formed from alternately overlapping oostegites arising from coxae 1-4 and 6; those of coxae 6 longest, extending posteriorly over pleopods; anteriorly directed flap on sternite 7 forms posterior pocket. Pleopod 1 laminar, peduncle lateral margin expanded, laminar. Pleopods 2-5 with peduncle medial margin massively branchiated; pleopod 3 with branchiae on endopod proximomedial angle. Endopods 3 and 4 with posterior surface lobed, endopod of pleopod 5 massively lobed and folded. Uropod rami extending beyond posterior of pleotelson.

**Composition.** *Livoneca bowmani* Brusca, 1981.

**Remarks.** *Livoneca*, regarded as one of the largest cymothoid genera, has grown steadily in size, since first established. If the synonymy of *Ichthyoxenus* (e.g. Miers, 1880; Monod, 1931; Fryer, 1965; Lincoln, 1972) were accepted, then at the present time 90 species would be included.

Although species were regularly added to the genus since its inception, very few workers since Schiödte & Meinert (1884) have attempted to diagnose the genus. The only recent attempts to diagnose *Livoneca* are those of Brusca (1981), and Bruce (1986). The problems posed by the genus are evident when one considers that of the 15 characters listed by Brusca (1981), 13 are qualified (i.e. multistate, or prefaced by words like usually, often, generally). Of the three unqualified characters, two were specifically contradicted by the species figured in that work. Bruce (1986) in the table of characters for *Livoneca* managed six qualified characters out of ten, but qualified the entire set of characters by stating that the diversity of morphology shown by *Livoneca* was incompatible with that normally shown by a single cymothoid genus.

It is now apparent that the uncritical placing of species into *Livoneca* was, in part, due to lack of descriptive data for the type species. Consequently generic diagnoses did not so much diagnose the genus *Livoneca*, but an amalgam of species that did not readily fit into other genera. Several of the related genera such as *Elthusa*, *Enispa*, *Ichthyoxenus* and *Idusa* were similarly poorly known, without adequate descriptions of their type species, and lacked intelligible diagnoses that would have allowed separation from *Livoneca*.

It is clear now (though not from the Latin diagnosis

of Schiödte & Meinert, 1884) that most valid species belong to *Elthusa*, and that most generic diagnoses (e.g. Richardson, 1905; Menzies, 1962; Menzies & Glynn, 1968; Brusca, 1981; Bruce, 1986) more effectively diagnose *Elthusa*.

*Livoneca*, here redefined, differs abundantly from all but one of the former species placed in the genus. The cephalic, pereopodal, pleopodal and pleonal morphology clearly identify it as belonging to the Anilocrinae (*sensu* Bruce, 1987c). Although this may seen a large departure from the lineages proposed by Brusca (1981), on morphological criteria it fits well. Furthermore, the morphological and parasite site differences between *Nerocila lomatia* Bruce, 1988 (a branchial parasite) and *Livoneca redmanii* are slight compared to those between *L. redmanii* and genera such as *Elthusa*, *Mothocya* or *Ichthyoxenus*.

There has been long running disagreement over the correct generic spelling, authors using *Livoneca* or *Lironeca*. Arguments for the two spellings can be found in Monod (1931:5) and Sivertsen & Holthuis (1980). Under the ICZN (third edition) *Livoneca* is clearly the correct spelling (Art 32c(ii)), and this spelling should be used in future.

There are no Australian species recorded for this genus.

## Marine Species Previously Placed in *Livoneca*

1. *L. atlantniroi* Kononenko, 1988. Recorded from the Bay of Biscay, here transferred to *Elthusa*.
2. *Ichthyoxenus asymmetrica* Ahmed, 1970. From Kor Abdullah, Arabian Gulf, Iraq; ectoparasitic, from an hypersaline habitat. The description and figures given for this species do not allow a generic or species assessment to be made.
3. *L. boscii* Bleeker, 1857. Malaysia, here transfered to *Catoessa* (types RMNH 67).
4. *L. bowmani* Brusca, 1981. East Pacific, differs from *L. redmanii* by having acute uropod apices. The only species other than the type species that is now retained in *Livoneca*.
5. *L. californica* Schiödte & Meinert, 1884. East Pacific, recently redescribed by Brusca (1981); here placed in *Elthusa*, but this species is in some ways similar to *Mothocya* (see Bruce, 1986).
6. *L. carryensis* Gourret, 1891. Trilles (1976b) includes this species as a synonym of *L. sinuata*.
7. *L. caudata* Schiödte & Meinert, 1884. Recorded only from Japan, here transfered to *Elthusa* (types RMNH 68).
8. *L. circularis* Pillai, 1954. Known only from India (Pillai, 1964). The generic position of this species is entirely uncertain, but it does not belong to any of the genera treated in this work.
9. *L. contracta* Miers, 1880. *Ceratothoa contracta* Miers, n.comb. is here transfered to *Ceratothoa*, the genus most appropriate for this species. The antennule, pereopod and pleon morphology all agree with *Ceratothoa* (sensu Bruce & Bowman, 1989), although the body shape is much wider. Known only from Mier's (1880) record from Australia (syntypes BMNH 1844: 105; 1846: 89).
10. *L. convexa* Richardson, 1905a. Redescribed by Brusca (1981), this species agrees totally with the genus *Enispa*. It differs from the only other species, *Enispa irregularis*, in having acute uropod apices. Brusca (1981) designated a neotype and neoallotype, but as that action did not meet the requirements of the ICZN (Art 75) with regard to habitat, host or nomenclatural problems, the neotype designation is invalid (see also comments under remarks for *Enispa irregularis*).
11. *L. cumulus* Haller, 1880. Now *Agarna cumulus*, see Trilles (1981) for synonymy.
12. *L. desmarestii* Leach, 1818. Synonym of *L. redmanii* (syntypes BMNH 1979: 33).
13. *L. dubia* Nierstrasz, 1918 and 1931. Nierstrasz (1918, 1931) published both accounts as new species (Bruce, 1987b); a synonym of *Renocila ovata*.
14. *L. ellipsoidea* Haller, 1880. There is no locality with the syntypes of this species, but examination of the types show this species to be a junior synonym of *L. redmanii* (syntypes MHNG).
15. *L. emarginata* Dana, 1853. Long accepted as a synonym of *L. redmanii* (see Trilles, 1976a).
16. *L. emarginata* Bleeker, 1857. East Indies. The type species for *Elthusa* (syntypes RMNH 66).
17. *L. engraulidis* (Barnard, 1936). Transfered to *Agarna* by Pillai (1954, 1965), later transfered to *Joryma* by Bowman & Tareen (1983).
18. *L. epimerias* Richardson, 1909. Synonym of *E. raynaudii*, present work.
19. *L. foveolata* (Hansen, 1897). Removed from *Irona* to *Livoneca* by Bruce (1986), the species is here transfered to *Elthusa*.
20. *L. frontalis* Richardson; 1910. Transfered to *Elthusa* (syntypes USNM 39504); Philippines.
21. *L. intermedia* Nierstrasz, 1931. Indonesia; I have not seen the type material of this species.
22. *L. indica* Edwards, 1840. Transfered to *Norileca*, present study.
23. *L. lata* Dana, 1853. Synonym of *L. redmanii*, present study.
24. *L. laticauda* Miers, 1877. Synonym of *E. raynaudii*, present study.
25. *L. longistylis* Dana, 1853. Accepted to be a synonym of *L. redmanii*, see Trilles (1976a) for synonymy.
26. *L. lunelli* Haller, 1880. Examination of the types show this species to be a synonym of *Elthusa emarginata* (syntypes MHNG).
27. *L. magna* Mañé-Garzón, 1979. Synonym of *E. raynaudii*, present study.
28. *L. mediterranea* Heller, 1868. Trilles (1976b) includes this Mediterranean species under the synonymy for *Livoneca sinuata*. This species is similar to *Livoneca sensu strictu*, but needs further

description before its correct generic position can be ascertained.

29. *L. menziesi* Brusca, 1981. East Pacific; transfered to *Elthusa*.
30. *L. methipia* Schiödte & Meinert, 1884. I have not seen the types of this species, but it appears to belong to *Elthusa*. Known only from Rio de Janeiro.
31. *L. micronyx* Miers, 1880. Mauritius; the habitat of this species is not known, but the morphology agrees with *Ichthyoxenus*.
32. *L. nanoides* (Stebbing, 1905). Transfered to *Livoneca* from *Irona* by Bruce (1986), now transfered to *Elthusa*.
33. *L. nasicornis* Nierstrasz, 1917. Long recognised as a synonym of *Argathona rhinoceros* (Family Corallanidae) (see Bruce, 1982).
34. *L. neocytta* Avdeev, 1975. To *Elthusa*, present work.
35. *L. novaezelandiae* Miers, 1874. Synonym of *E. raynaudii*, present work.
36. *L. ochotensis* Kussakin, 1979. Transfered to *Elthusa*; this species is very similar to *E. raynaudii*. Sea of Ochotsk.
37. *L. olivacea* De Kay, 1844. Listed as a synonym of *L. ovalis* by Kussakin (1979) and on that basis here included as a synonym of *L. redmanii*.
38. *L. ornata* Heller, 1868. Listed as a junior synonym of *L. indica* by Trilles (1976a). I have not seen the type material for this species and can make no comment.
39. *L. ovalis* (Say, 1818). Synonym of *L. redmanii*, Trilles (1976a) and present study.
40. *L. panamensis* Schiödte & Meinert, 1884. Synonym of *Elthusa vulgaris*, see Brusca (1981) for synonymy.
41. *L. parva* Nierstrasz, 1915. Transfered to *Elthusa* (holotype RMNH 71); Indonesia.
42. *L. philippinensis* Richardson, 1910. Transfered to *Elthusa* (types USNM 40916); Philippines.
43. *L. plagulophora* Haller, 1880. Transfered to *Mothocya* by Bruce (1986).
44. *L. pomatoi* Gaillat Airoldi, 1940. *Incerta sedis*, current descriptions of this species do not allow for generic assessment; most recently treated by Trilles (1976b); Mediterranean.
45. *L. pontica* Borcea, 1933. Probable synonym of *Mothocya taurica*, see Bruce (1986) for discussion; Mediterranean.
46. *L. propinqua* Richardson, 1910. To *Elthusa*, present work.
47. *L. pterygota* Koelbel, 1879. Synonym of *Agarna cumulus*, see Trilles (1981).
48. *L. puhi* Bowman, 1962. This species is most similar to *Ichthyoxenus minabensis*, from which it differs by having a bluntly rounded anterior margin to the cephalon, wider pleon and narrower uropod exopod. As it agrees with the diagnosis given here for *Ichthyoxenus* it is transfered to that genus. *L. puhi* was collected from moray eels.
49. *L. punctata* Uljanin, 1872. Probable synonym of *Mothocya taurica*, see Bruce (1986) for discussion.
50. *L. raynaudii* Edwards, 1840. To *Elthusa*, present work.
51. *L. rafineskii* Leach, 1818. Examination of the syntypes (BMNH 1979: 338) show this to be a synonym of *L. redmanii*, not of *E. raynaudii* as suggested by some authors (Sivertsen & Holthuis, 1980; Trilles, 1976a).
52. *L. redmanii* Leach, 1818. Type species for the genus; Caribbean.
53. *L. renardi* Bleeker, 1857. Belongs to *Mothocya*, see Bruce (1986) for synonymy.
54. *L. reniformis* Menzies & Frankenberg, 1966. The description of this species does not allow for generic assessment, it may belong to *Idusa*; Georgia, USA.
55. *L. ricinoides*. Referred to by Risso (1816), current status uncertain.
56. *L. sacciger* Richardson, 1909. To *Elthusa*, present study.
57. *L. samariscii* Shiino, 1955. Transfered to *Elthusa*; the species clearly does not belong to *Livoneca*, but the description is not sufficiently detailed to be sure of its generic position; Japan.
58. *L. samoensis* Schiödte & Meinert, 1884. Transfered to *Elthusa*; Samoa. I have not seen the types of this species.
59. *L. sinuata* Koelbel, 1879. Trilles (1976b) places the older name *L. mediterranea* as a questionable synonym; Mediterranean.
60. *L. soudanensis* Richardson, 1911. *Incerta sedis*; there exists only a brief description without figures for this West African species; Trilles (1976a) has given a photograph of the holotype.
61. *L. splendida* Moreira & Sadowsky, 1981. Brazil. Very similar to *E. raynaudi*, appearing to differ only in having the posterior margin of pereonite 7 more deeply indented.
62. *L. stewarti* Filhol, 1885. Synonym of *E. raynaudii*, present study.
63. *L. taurica* (Czerniavsky, 1868). Transfered to *Mothocya* by Bruce (1986), the status of this species and synonyms is uncertain; Black Sea.
64. *L. tenuistylis* Richardson, 1912. Atlantic Panama. From Richardson's (1912) description and figures and that the position on the host was between pectoral and pelvic fins, it would appear that this species belongs with one of the externally attaching anilocrine genera.
65. *L. texana* Pearse, 1952. *Incerta sedis*; I have not seen the type material, nor any adequate figures for this species; Gulf of Mexico.
66. *L. triangulata* Richardson, 1910. To *Norileca*, present work.
67. *L. triloba* De Kay, 1844. Listed in the synonymy of *L. ovalis* Kussakin (1979), and therefore now accepted as a synonym of *L. redmanii*.
68. *L. tropicalis* Menzies & Kruczynski, 1983. Transfered to *Elthusa*; Gulf of Mexico.
69. *L. turgidula* Hale, 1926. To *Elthusa*, present work.
70. *L. vulgaris* (Stimpson, 1857). Transfered to *Elthusa*; an East Pacific species, recently redescribed by Brusca (1981).

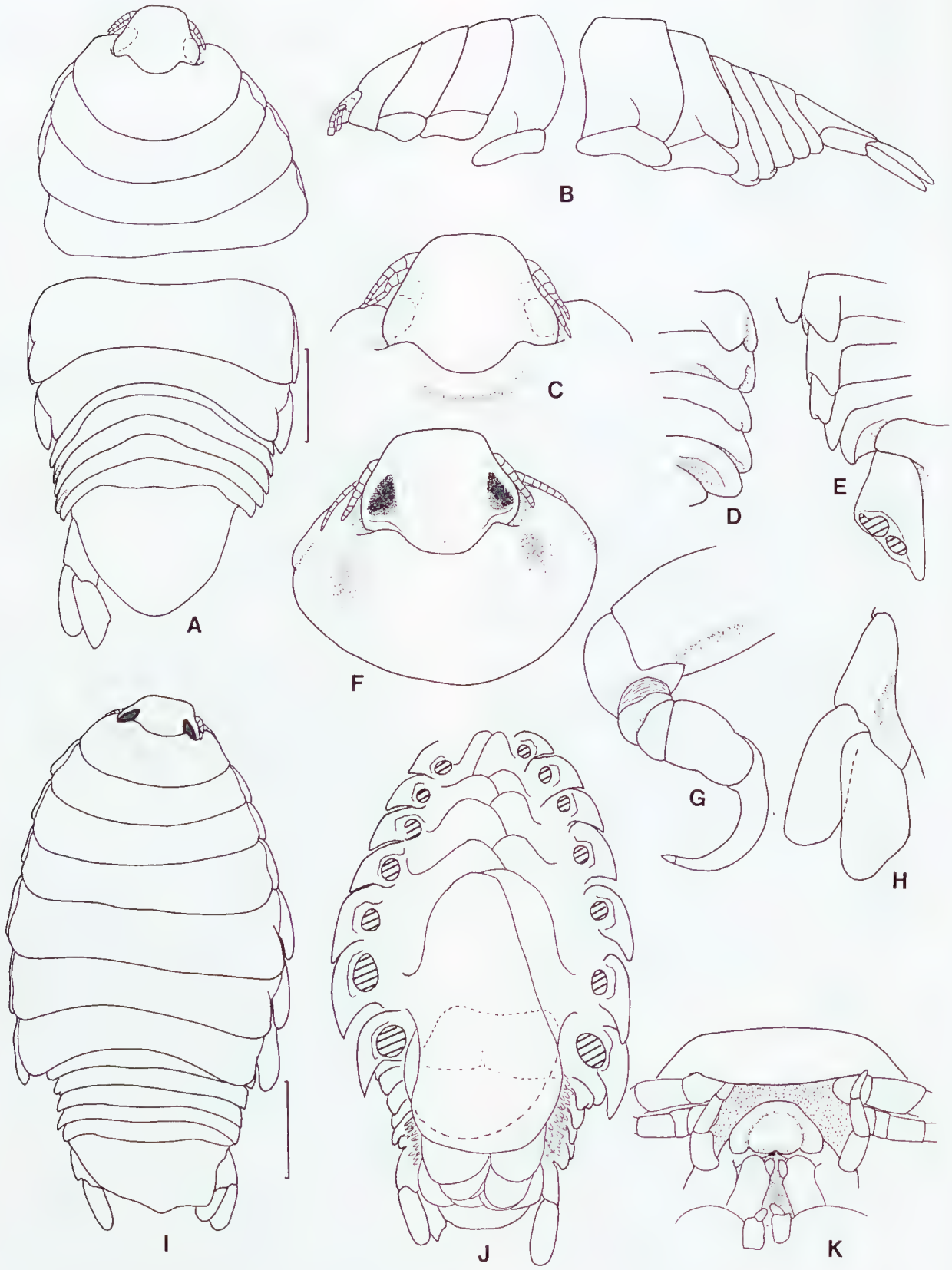


**Fig.26.** *Livoneca redmanii*. A–D, G, H, holotype, remainder female #1, USNM 171630. A, dorsal view; B, lateral view; C, cephalon; D, right pleonites, dorsolateral view; E, right pleonites, ventral view; F, head, pereonite 1; G, pereopod 1; H, left uropod, *in situ*; I, dorsal view; J, ventral view of brood pouch; K, frons. Scale line represents 4.0 mm.

### *Livoneca redmanii* Leach

Figs 26,27

*Livoneca Redmanii* Leach, 1818: 352.–Desmarest, 1825: 308.–Lucas, 1850: 251.
*Livoneca Desmarettii* Leach, 1818: 352 (lapsus).
*Livoneca Rafineskii* Leach, 1818: 352.–Desmarest, 1825: 308.
*Cymothoa ovalis* Say, 1818: 394.–de Kay, 1844.
*Livoneca Desmarestii*.–Desmarest, 1825: 308.–Edwards, 1839: pl.66, fig.3a-e.–Edwards, 1840: 261.–Lucas, 1850: 251.
*Livoneca Desmaresti*.–Bosc, 1830: 146.–Gerstaecker, 1882: 267.
*Livoneca Redmanii*.–Edwards, 1839: pl.66, figs 4-4a.–Edwards, 1840: 261.
*Cymothoa triloba* de Kay, 1844: 46, pl.10, fig.40.
*Lironeca Redmanii*.–White, 1847: 109.
*Lironeca Desmarestii*.–White, 1847: 109.
*Lironeca Raffineskii*.–White, 1847: 109.
*Lironeca ovalis*.–White, 1847: 109.–Alperin, 1966: 122.–Menzies & Frankenberg, 1966: 9.–Schultz, 1969: 164, fig.249.–Overstreet, 1978: 48, fig.49.–Williams & Williams, 1979: 123.–Kussakin, 1979: 296, figs 162,163.–Moreira & Sadowsky, 1979: 111.–Ellis, 1981: 124.
*Livoneca rafineskii*.–Lucas, 1850: 251.
*Livoneca longistylis* Dana, 1853: 754, pl.50, fig.3a-b.
*Livoneca emarginata* Dana, 1853: 755, pl.50, fig.4a-b (not *L. emarginata* Bleeker, 1857).
*Livoneca lata* Dana, 1853: 756, pl.50, fig.51-c.
*Livoneca ovalis*.–Harger, 1873: 572, pl.6, fig.29.–Harger, 1880a: 162.–Harger, 1880b: 395, 428, 434, pl.11, fig.67a-f.–Gerstaecker, 1882: 267.–Stebbing, 1893: 352.–Richardson, 1900: 222.–Richardson, 1905: 263, figs 276,277.–Rathbun, 1905: 4, 39.–Summer, Osborn & Cole, 1913: 658.–Light, 1937: 71, figs 1-4.–Behre, 1950: 18.–Miner, 1950: 442, pl.143.–Briggs, 1970: 55.
*Livoneca ellipsoidea* Haller, 1880: 386, pl.18, figs 16,17.
*Livoneca Redmanni*.–Gerstaecker, 1882: 265.–Schiödte & Meinert, 1884: 353, pl.14, figs 6-12.–Stebbing, 1893: 352.
*Livoneca redmanni*.–Richardson, 1905: 261, figs 274,275.–Van Name, 1925: 462.–Gurjanova, 1936: 86.–Menzies, 1962: 115.–Kussakin, 1979: 294.
*Lironeca redmanni*.–Hutton, 1964: 447.–Menzies & Frankenberg, 1966: 9.–Menzies & Glynn, 1968: 46, fig.4D-G.–Schultz, 1967: 163, fig.247.–Menzies & Kruczynski, 1983: 40, 58.
*Lironeca redmanii*.–Trilles, 1976a: 774, pl.1, fig.2.–Trilles, 1981: 594, pl.4, figs 19-22.
*Lironeca redmani*.–Ellis, 1981: 124.

**Material examined.** HOLOTYPE (about 25.0, in 2 pieces), Jamaica (Whites Ms catalogue no 213), coll. Redman, presented by W.E. Leach (BMNH 1979:410.1). 2 females, syntypes of *L. ellipsoidea*, no original label (MHNG). 5 females (ovigerous 21.0, 22.0, 22.0, 23.0), male 15.0, Gulf of Morrosquillo, Colombia, about 9°30'N 76°21'W, 28 Nov. 1968, from gills of *Scomberomorus cavalla* (King Mackeral) (USNM 171630).

**Remarks.** Detailed figures are given here to fully illustrate the generic characters of *Livoneca*. Similarly the species can be identified from these figures. It can be seen from the synonymy that *Livoneca redmanii* is a widely recorded species, with a distribution extending from the Caribbean along the eastern United States seaboard as far north as Wood's Hole, Massachusetts (Richardson, 1905). It can easily distinguished from the only congener, the allopatric *Livoneca bowmani* by bluntly rounded rather than acute uropod apices.

### *Norileca* n.gen.

**Type species.** *Livoneca indica* Milne-Edwards, 1840.

**Diagnosis of female.** Body weakly vaulted, twisted to one side. Cephalon posterior margin weakly or not trilobed. Coxae narrow, those of pereonites 3-7 shorter than respective segment; those of 5-7 as long as respective segment. Pleon not immersed in pereon; pleonite 1 longest; pleonites 1-5 becoming progressively narrower.

Antennule subequal to, or shorter than antenna, bases set wide apart. Mandible palp article 2 flattened, greatly expanded. Maxilliped without oostegital lobes. Pereopods without expanded lobes; bases without expanded carina. Brood pouch made up from pairs of alternately overlapping oostegites arising from coxae 2-5. Pleopods 1-4 with laminar rami; peduncles 2-5 with laminar lobe on lateral margin; endopods 3-5 with folded proximomedial lobe; endopod 5 with 2 large folded lobes, distal margin medially indented. Pleopods 1-5 progressively increasing in size.

**Composition.** *Norileca triangulata* (Richardson, 1910) n.comb.

**Remarks.** This genus is most similar to *Livoneca* with which it shares a similar pereopod, cephalon and pleon morphology. *Norileca* has the cephalon weakly trilobed, and the lateral margin of pleonites 1 to 3 are never bilobed. Other major differences to *Livoneca* are the expanded mandible palp article, lack of folds on endopods of pleopods 3 and 4 and lack of branchiated pleopod peduncles.

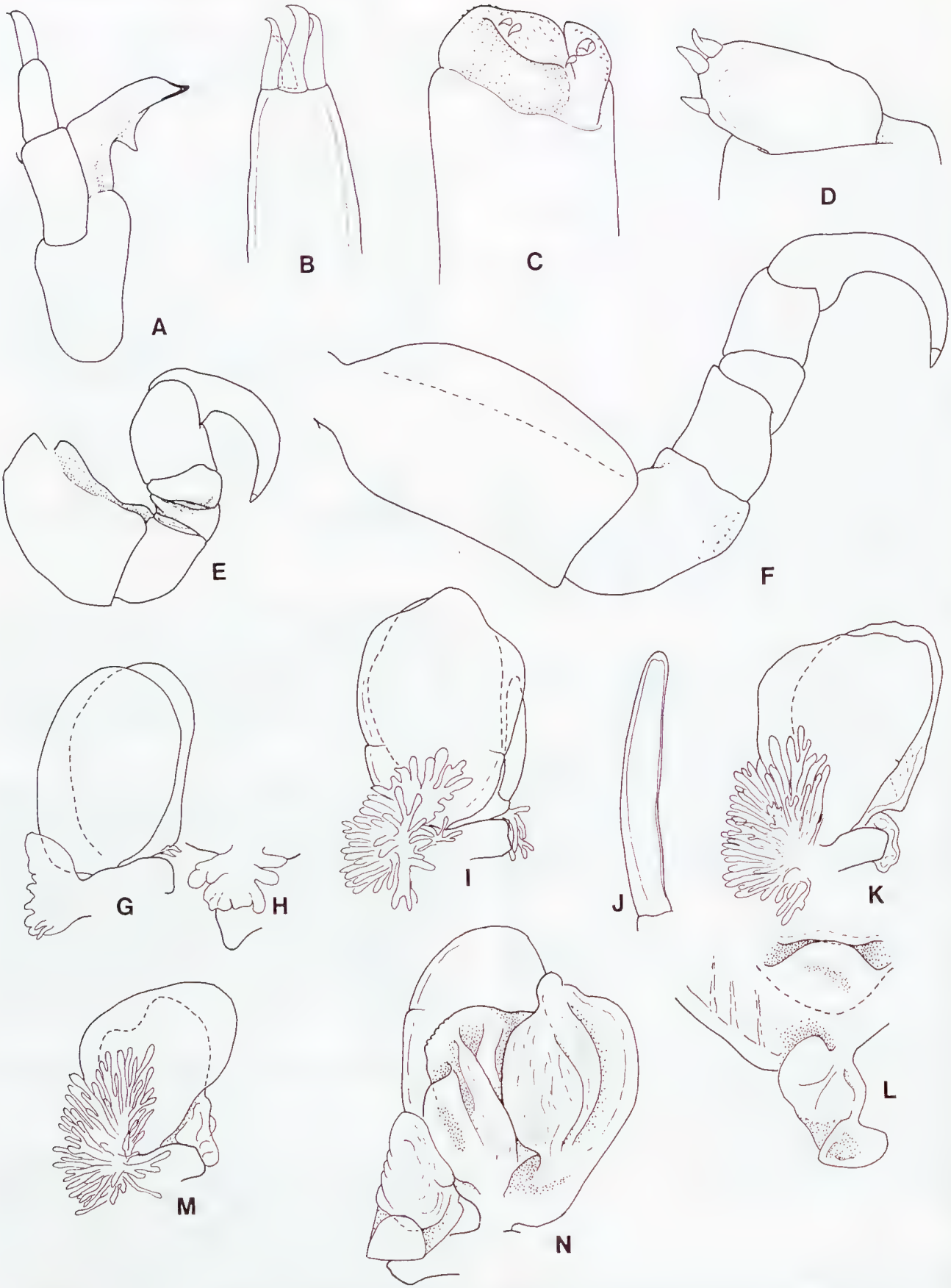


**Fig.27.** *Livoneca redmanii*. All figs of female #1, USNM 171630. A, mandible; B, maxillule apex; C, maxilla apex; D, maxilliped article 3; E, pereopod 1; F, pereopod 7 (dashed line indicate start of carina); G, pleopod 1; H, pleopod 1 endopod, dorsal proximomedial angle; I, pleopod 2; J, appendix masculina; K, pleopod 3; L, pleopod 3 endopod, dorsal proximomedial angle; M, pleopod 5; N, pleopod 5 dorsal view (branchiae omitted).

## Key to the Species of *Norileca*

1. Body weakly twisted to one side, pleonite 5 manifestly narrower than pleonite 1; maxilliped palp article 2 about as long as article 3 ..... *N. triangulata*

—— Body twisted to one side, pleonite 5 about as wide as pleonite 1; maxilliped palp article 2 about 3 times as long as article 3 ..... *N. indica*

### *Norileca indica* (Milne-Edwards) n.comb.

Figs 28, 29

*Livoneca indica* Milne-Edwards, 1840: 262.–Bleeker, 1857: 21.–Gerstaecker, 1882: 261.–Schiödte & Meinert, 1884: 362, pl.15, figs 3-6.–Richardson, 1910: 24.–Nierstrasz, 1915: 99.–Nierstrasz, 1931: 142.–Borcea, 1933: 482.–Beumer, *et al.*, 1982: 33.

*Lironeca indica*.–Trilles, 1976: 77, pl.2, fig.3.–Trilles, 1979: 266.–Avdeev, 1978: 281.–Rokicki, 1982: 205, figs 1, 2.

*Livoneca ornata* Heller, 1868: 145, pl.12, fig.15.–Gerstaecker, 1882: 261.

**Material examined.** Female (non-ovigerous 17.0), male (11.0), Table Head, Port Essington, Cobourg Peninsula, NT, 11°14'S 132°11'E, 10 Sept. 1985, surface night light, coll. R. Williams (NTM Cr6700). Male (11.0), as previous, but on *Herklotichthyes* sp. (NTM Cr4051). Female (non-ovigerous 28.0), Arafura Sea, NT, 10°26.5'S 136°07.0'E, 22 Nov. 1980, in gill chamber of *Selar crumenophthalmus* (AM I21956-006), 58 m depth, coll. AM, FRV *Soela* (AM P37760).

**Additional material examined.** 3 females, 2 males, *Siboga* Expedition Stn 172, Gisser, 26-28 Aug. 1899, reported on by Nierstrasz (1931) (ZMA). All Arafura Sea. Female, 10°22'S 136°35'E, 12 Nov. 1986, coll. W. Houston (NTM Cr4646). Female, 10°08.3'S 136°45.5'E, 17 Mar. 1985, coll. W. Houston (NTM Cr3263). Male, BYBE 2, 19 June 1987, 80 m (NTM Cr5886). Female, 10°20'S 134°22'E, 11 June 1987, 59 m, coll. NT Fish. Observer (NTM Cr5889).

**Type material.** Holotype held at the Muséum Nationale d'Histoire Naturelle, Paris.

**Type locality.** Milne-Edwards (1840) gave Sumatra as the type location.

**Description.** Body about 2.4-2.5 times as long as wide, twisted to one side; widest at pereonite 4; dorsum moderately convex with ill-defined longitudinal median ridge. Cephalon not deeply immersed in pereonite 1, anterior margin subtruncate; eyes 0.47-0.52 width of cephalon. Pereonite 1 with posterolateral angles weakly produced. Coxae of pereonite 2 as long as segment; coxae of pereonites 3-7 all about 0.8 as long as respective segment. Posterior margin of pereonite 7 weakly concave. Pleon 0.66-0.74 width of pereonite 4, with all segments about as wide as pereonite 7, pleonite 5 as wide as pleonite 1; lateral margins posteriorly directed. Pleotelson triangular, anteromedial surface vaulted.

Antennule extending to pereonite 1, bases set wide apart, composed of 8 articles; antenna slightly longer than antennule, with 9 articles. Mandible with large palp, article 2 flattened, expanded; article 3 0.35 as long as article 2. Maxilliped article 3 with 4 large recurved spines.

Pereopod 1 ischium 0.69 length of basis; dactylus curving abruptly at about proximal 0.2 of its length, extending to anterior of carpus, which has recess that receives dactylus apex. Pereopods 2 and 3 similar to 1 but slightly longer. Pereopods 4-7 similar to each other; pereopod 7 ischium 1.03 length of basis, dactylus extends to posterior of carpus which has recess that receives dactylus apex; propodal palm with 2 small spines.

Pleopods not examined in detail, but appear essentially the same as that of male, but appendix masculina absent. Uropods about 0.55-0.60 length of pleotelson, rami subequal in length, apices rounded; endopod slightly tapered.

**Male.** Body not twisted, lateral margin sub-parallel. Coxae longer than in female. Pleon 0.73 width of pereon. Uropods about 0.8 length of pleotelson. Pereopod 1 with 5 small spines on propodal palm. Pleopod 1 peduncle with lateral lobe, pleopods 2-5 with peduncle lateral lobe expanded. Pleopod 2 with appendix masculina as long as endopod. Pleopods 3-5 endopods with folded proximomedial lobe. Pleopod 5 endopod distal margin medially indented, posterior surface complexly folded.

**Colour.** Pale brown, black chromatophores over dorsal surface, particularly on pleon, and also pleotelson which appears black.

**Size.** Present material 17-28 mm, Trilles (1976) reports 18-33 mm for ovigerous females, and records 13 non-ovigerous females (without locality) from 10.5-17.0 mm. It is possible that the smaller of these could be *L. triangulata*.

**Variation.** In both female specimens, the pleotelson is distorted. The specimen from *Selar crumenophthalmus* has a more distinct mediodorsal ridge, and has the

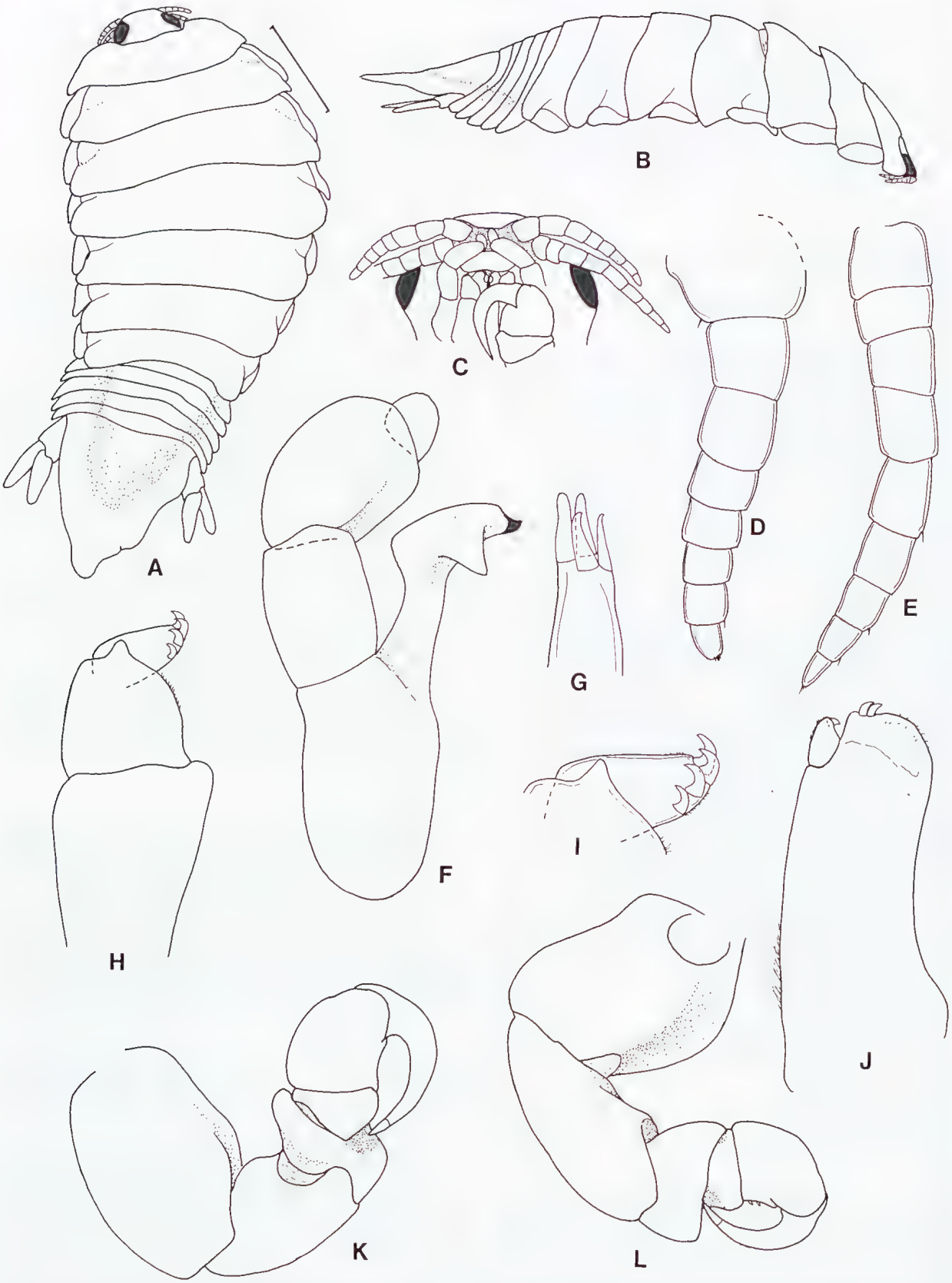


**Fig.28.** *Norileca indica*. All figs of female 17.0 mm NTM Cr6700. A, dorsal view; B, lateral view; C, frons; D, antennule; E, antenna; F, mandible; G, maxillule apex; H, maxilliped; I, maxilliped article 3; J, maxilla; K, pereopod 1; L, pereopod 7. Scale line represents 3.0 mm.

pleonites more strongly produced.

**Remarks.** This species can easily be distinguished from *Norileca triangulata* by the larger size, twisted body shape, straight sided pleon, shorter uropods and shorter mandible palp article 3.

The pleopods of both females were damaged and fragile, and could not be dissected and described. Pleopods of females always have the folding on the lobes more developed than males. As can be seen the folding and lobes are already well developed in the male specimen and females will have similar pleopods but with more complex folding.

**Hosts.** *Selar crumenophthalmus* and *Herklotichthyes* sp. The specimen on *S. crumenophthalmus* was positioned ventrally in the gill cavity, cephalon to the anterior with the sternum facing out (i.e. laterally) (see fig. 1, Rokicki, 1982); three pereopods had their dactyli hooked around the gill operculum. The gill itself was considerable atrophied. Avdeev (1978) recorded *Atule melan* and *Rasteliger kanangurta*; Rokicki (1982) recorded *Selar crumenophthalmus*.

**Distribution.** Present material is all from the Arafura Sea, off the Northern Territory coast. Previous records Sumatra, Indonesia, Philippines and New Guinea (Trilles, 1976) and off Mozambique (Rokicki, 1982). Avdeev (1978) lists the species from north-western Australia.

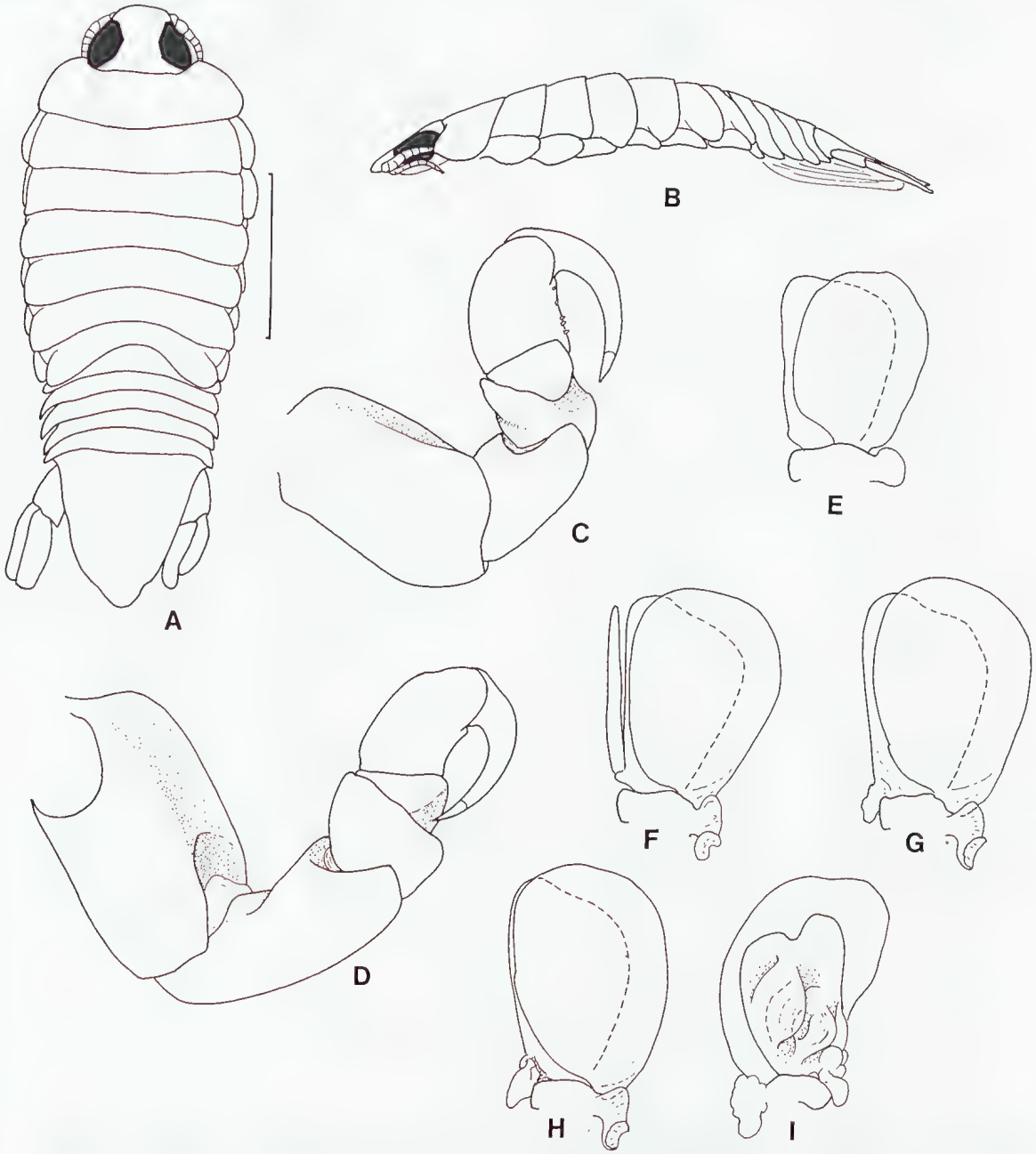


**Fig.29.** *Norileca indica.* All figs of male 11.0 mm, NTM Cr4051. A, dorsal view; B, lateral view; C, pereopod 1; D, pereopod 7; E–I, pleopods 1-5 respectively. Scale line represents 3.0 mm.

***Norileca triangulata*** (Richardson) n.comb.

Figs 30, 31

*Livoneca triangulata* Richardson, 1910: 23, fig.22.– Nierstrasz, 1931: 143.

**Material examined.** Syntypes, 2 females (ovigerous 9.2, 9.5), male (9.0), Tanimdao Island, Philippine Islands, 25 Feb. 1908, anchorage, at night light, US Bureau of Fisheries Philippine Albatross Expedition 1907-8 (USNM 40915).

**Australian material.** Female (non-ovigerous 12.5), Eel Reef, Cape York, Qld, 12°32'S 143°32'E, 20 Feb. 1979, surface light over 55 m, gill of *Parexocoetus brachypterus* coll. AM-AIMS (AM P37759). Female (non-ovigerous 12.0), 2 males (7.5, 9.0), off Michaelmas Cay, Great Barrier Reef, 16°42'S 146°10'E, May-June 1926, on *Parexocoetus brachypterus* (Fish No. IA-2784, IA-2786), coll. T. Iredale & G.P. Whitley (AM P37737), P37758). Female (ovigerous 17.5), Mooloolabah, south-eastern Qld, 2 May 1985, on gills of *Sardinella gibbosa*, coll. C. Keenan (QM W13112).

**Type locality.** Tanimdao Island, Philippines (Richardson, 1910).

**Description of Australian females.** Body 2.2-2.5

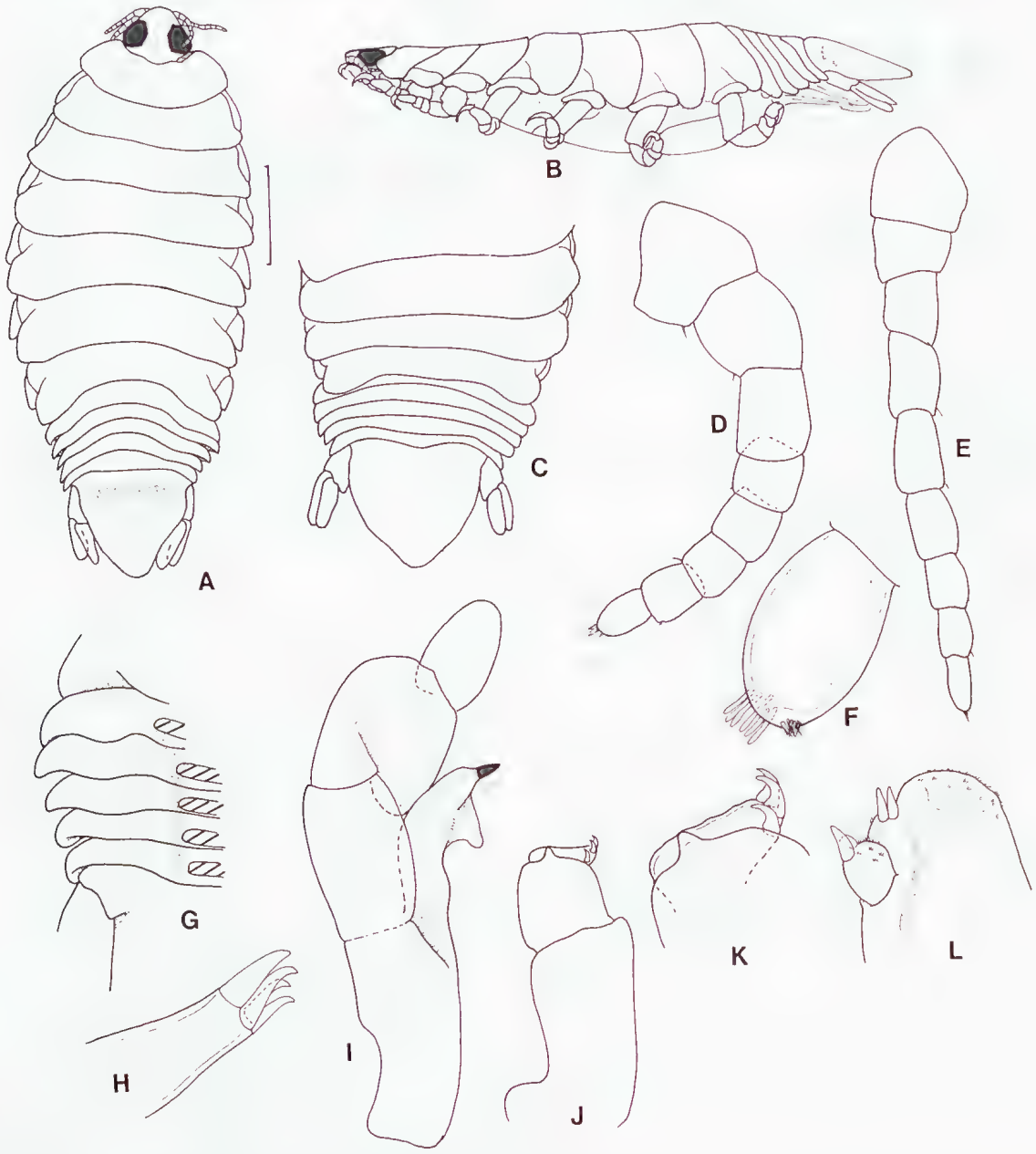


**Fig.30.** *Norileca triangulata*. All figures of female ex *Sardinella gibbosa*, except C. A, dorsal view; B, lateral view; C, posterior, female 12.5 mm Cape York; D, antennule; E, antenna; F, antennule terminal article; G, right pleonites, ventral view; H, maxillule apex; I, mandible; J, maxilliped; K, maxilliped article 3; L, maxilla apex. Scale line represents 3.0 mm.

times as long as wide, weakly twisted; widest at pereonite 4 or 5; dorsum weakly convex. Cephalon not deeply immersed in pereonite 2; eyes 0.6-0.7 width of cephalon; anterior margin smoothly rounded, not turned down. Coxae of pereonite 2 as long as segment; those of pereonites 3-4 shorter than respective segment. Coxae all narrow, from 0.46 as wide as long (pereonite 2) to 0.23 as wide as long (pereonites 4-6). Pereonite 7 posterior margin with moderate indentation. Pleonite 1 longest, as wide or slightly wider than pereonite 7; pleonite 5 distinctly narrower than 1 (0.75-0.83 or wider). Pleotelson triangular.

Antennule bases set widely apart; extends to pereonite 2, composed of 8 articles. Antenna slightly longer, with 9 articles. Mandible palp large, article 2 expanded; article 3 0.77 as long as article 2. Maxillule with 4 terminal spines. Maxilla with 2 spines each on medial and lateral lobes. Maxilliped with laminar lobes; article 3 with 3 large recurved spines.

Pereopod 1 with ischium 0.80 as long as basis; propodus with 5 spines on palm; dactylus abruptly angled at proximal 0.2, extending to merus. Pereopods 2 and 3 similar to 1, but pereopod 2 with 3 spines on propodal palm, and pereopod 3 without. Pereopods 4-7 similar to each other, all bases with distinct anterolateral carina. Pereopod 7 basis and ischium subequal in length; dactylus extending to posterior of carpus.

Pleopod 1 rami round, peduncle lateral lobe weakly developed; pleopods 2-5 with peduncle lateral lobe well developed. Pleopods 3-5 endopods with folded

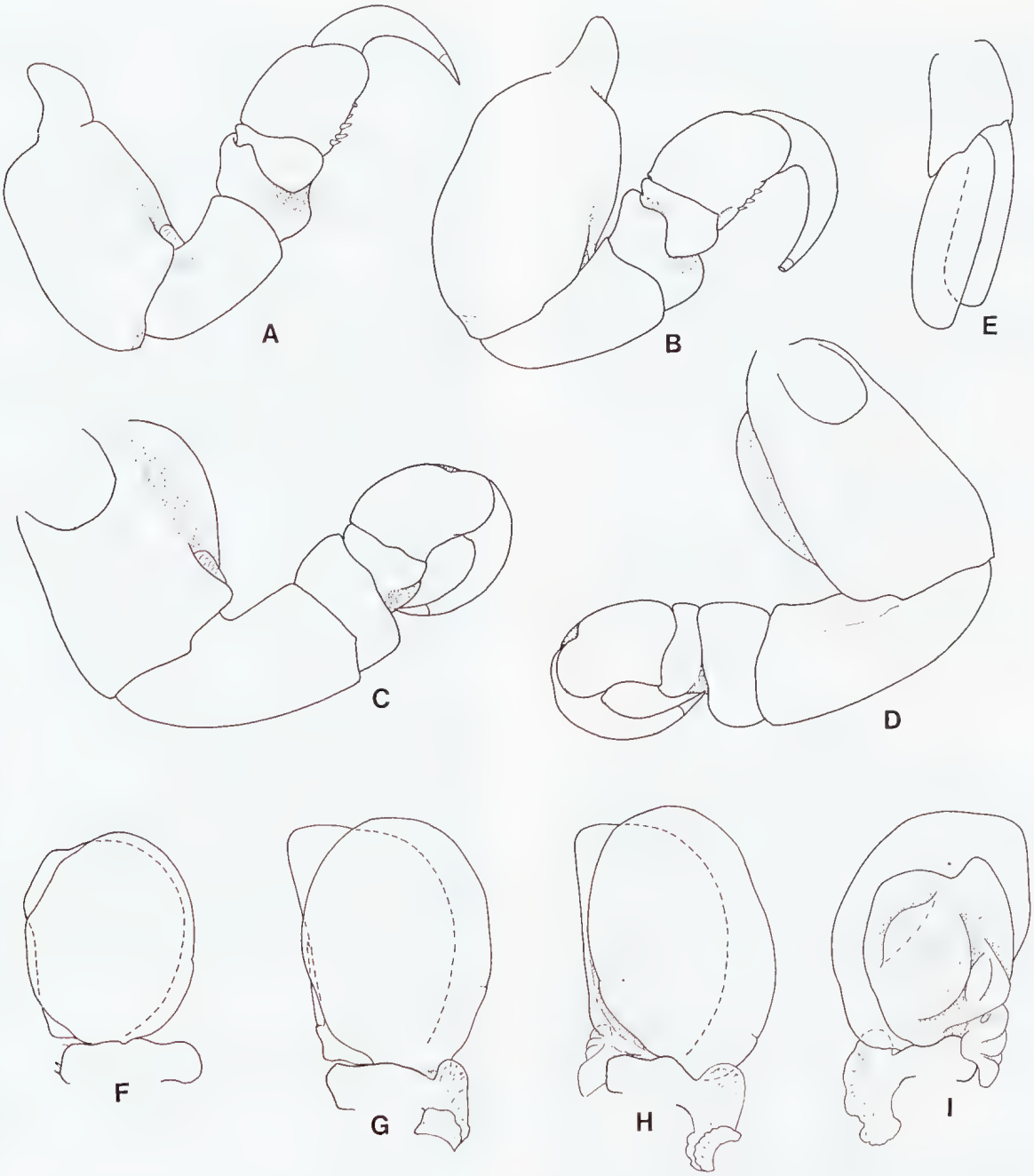


**Fig.31.** *Norileca triangulata*. All figs of female ex *Sardinella gibbosa*. A–D, pereopods 1, 2, 6, 7 respectively; E, uropod; F–I, pleopods 1, 2, 4, 5 respectively. Scale line represents 3.0 mm.

proximomedial lobe; pleopod 5 endopod posterior surface complexly folded. Uropods about 0.75 length of pleotelson, endopod slightly longer than exopod, both rami subequal in length.

**Male.** Both males (a pair from one host) are in very poor condition, but appendages do not differ significantly from those of the females.

**Colour.** Pale tan in alcohol, with chromatophores thinly spread on dorsal surfaces.

**Size.** Ovigerous females from 9.2-17.5 mm, males 7.5-9.0mm.

**Remarks.** This species is characterised by a nearly flat dorsum, large eyes, cephalon weakly immersed in pereonite 7, weakly twisted body, mandible palp article 2 greatly expanded, pleonite 5 narrower than 1 and triangular pleotelson.

*Norileca triangulata* can be distinguished from *N. indica* by several characters, the easiest to observe being the nearly straight body, larger eyes, pleonite 5 narrower than 1 and the proportionally longer uropods. Other characters are discussed under the 'Remarks' for *N. indica*. A further difference between the two species is that *N. triangulata* attaches with sternites innermost, while *N. indica* attaches with sternites outermost. Host and capture data indicate that both species occur on surface schooling fishes.

**Hosts.** Present material from *Parexocoetus brachypterus*, *Sardinella gibbosa*.

**Distribution.** Philippine Islands (Richardson, 1910); present material from Queensland — Eel Reef, Cape York; Michaelmas Cay, near Cairns; and Mooloobah, south-eastern Queensland.

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# A Radiation of Hydrobiid Snails in Threatened Artesian Springs in Western Queensland

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Abstract. A radiation of hydrobiid snails exhibiting diverse morphology is described from western Queensland. All but one of the species live in springs west of the Great Dividing Range, most of them derived from water emanating from the Great Artesian Basin. Twelve species contained in the genus *Jardinella* are described from eight springs or small spring groups, spread over an area of about 260,850 km$^2$. Most of the species are found in springs that are highly vulnerable to damage and are thus under threat of extinction. Only one species is located in a protected area. The 12 species, all of them new, are discriminated primarily using shell and anatomical characters. A cladistic analysis is used to indicate the probable evolution of the group which is shown to be a monophyletic radiation separated from related genera on opercular and genital morphology. Discriminate analysis shows that the species can be distinguished on shell characters alone. Seven allopatric species are found in separate springs or small groups of springs, the remaining five (and a sixth undescribed species) live in Edgbaston Springs, all six species living sympatrically in at least one of these springs. The genus *Jardinella* is thought to consist of the relictual endpoints of a radiation that commenced in the (mid?)Tertiary. The type species is found in coastal streams and rivers in north Queensland and represents a rather derived member of the group. All but one of the spring-associated species is considered to be endangered because the springs in which they are found have no conservation status and are threatened by pastoral activities and drawdown caused by artesian bores.

Ponder, W.F. & G.A. Clark, 1990. A radiation of hydrobiid snails in threatened artesian springs in western Queensland. Records of the Australian Museum 42(3): 301–363.

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Permanent arid-zone springs are known to be sites of some spectacular radiations of aquatic animals, examples being the pup fishes of western North America (Deacon & Minckley, 1974) and hydrobiid snails in the Cuatro Ciénegas Basin, Coahuila, Mexico (Hershler, 1985). Recently Ponder *et al.* (1989) demonstrated a significant radiation of hydrobiids from springs near the south-western side of Lake Eyre South in South Australia.

While the fishes of artesian springs associated with the Great Artesian Basin (GAB) have been rather well studied (see Glover, 1982 and 1989 for references) the invertebrate fauna is only belatedly gaining some attention (Ponder, 1985, 1986; Mitchell, 1985). An account of the natural history of Dalhousie Springs in the far north of South Australia has been recently published with information on the aquatic fishes, crustaceans and molluscs (Zeidler & Ponder, 1989) but there is only one brief report on the endemic invertebrates in artesian springs in Queensland (Ponder, 1986).

The conservation importance of the artesian springs associated with the Great Artesian Basin has recently been discussed by Harris (1981), Ponder (1985, 1986, in press) and Zeidler & Ponder (1989). Work on their faunas is hampered by their inaccessibility and public awareness is slight, partly because of their remoteness and partly because most of the endemic fauna has a small body size and much of it remains undescribed. The fragility of these environments is not reflected by their conservation status. Only one group of South Australian artesian springs is located in a National Park and, similarly, of the Queensland springs that contain endemic fauna dealt with in this report, only one group is located within a National Park. All of the remaining artesian springs associated with the Great Artesian Basin are located on pastoral land and are thus potentially threatened by pastoral activities.

There is little published information on the geology and hydrology of Queensland artesian springs but Habermehl (1982) and Ponder (1986) review the literature. Habermehl (1982) recognises six spring-groups in Queensland which he names, and this classification is followed by Ponder (1986) who refers to the spring-groups as spring supergroups (see also Figure 1).

The present study is based on material collected during a survey of Queensland artesian springs in 1984 with some additional material collected in 1988. There remain many springs that are yet to be visited and it is very likely that additional species will eventually be found.

## Materials and Methods

Material for this paper results from two collections, one in September to October 1984 by W.F. Ponder and P.H. Colman (with M.A. Habermehl) and the other in May 1988 by W. and L. Zeidler. A list of stations is given in Appendix 1. The station numbers cited are those assigned in the field. The hydrological data for the 1984 stations will be published separately by M.A. Habermehl. Some of the sites containing hydrobiids are illustrated in Figures 2 and 3. All tables referred to thoughout the text are listed in Appendix 2.

Collections were made by hand using a small sieve (approximately 1 mm mesh) and by washing substratum (rocks, wood, vegetation etc.) into a plastic bowl. The untreated residue was left to stand over night in water taken from the collection site with a few menthol crystals added to narcotise the snails. The sample was then fixed in 10% neutral formalin and the residue later sorted in the laboratory. In localities where more than one species was present numbers of each species were recorded and percentage frequencies calculated.

A subsample of adult shells (i.e. at terminal growth) was chosen from each sample randomly (see Table 3 for number measured from each sample). They were measured using a digitising pad linked to a microcomputer, a program automatically converting the input to millimetres. These data were utilised in constructing the descriptions and subjected to discriminate analysis.

The shell parameters measured were shell length, shell width, length of body whorl, length of aperture, width of aperture, width of umbilicus, and protoconch diameter. In addition the spire angle was calculated by the

computer from points entered along the spire, and the slope of the outer lip was determined in a similar manner. The whorl convexity was determined at the junction of the last whorl with the penultimate whorl and was estimated by the calculation of a convexity ratio. Three points were entered via the digitising pad, one at the middle of the whorl outline and one at each of the sutures above and below this point. The length of a line (a) from the middle of the outer edge of the whorl vertical to a line (b) drawn between the two sutures at the junction of the penultimate and body whorls was calculated by the computer and the ratio a/b (the convexity ratio) then determined. The number of protoconch and teleoconch whorls were counted.

The shells of the measured individuals were then gently cracked and the animals sexed after being removed from their shells. The operculum of each individual was removed from the foot, and the length, the distance of the nucleus from the edge opposite the end of the last whorl (i.e. at half the last whorl) and the length of the white smear (if one was present) were measured using the digitising pad.

Some shells (including juveniles for protoconch details) were mounted for scanning electron microscope (SEM) examination after cleaning with a mild solution of bleach and using an ultrasonic cleaner.

Heads (including penes in the case of males) and female genitalia were prepared for SEM examination using critical point drying. The shell was dissolved in dilute HCl

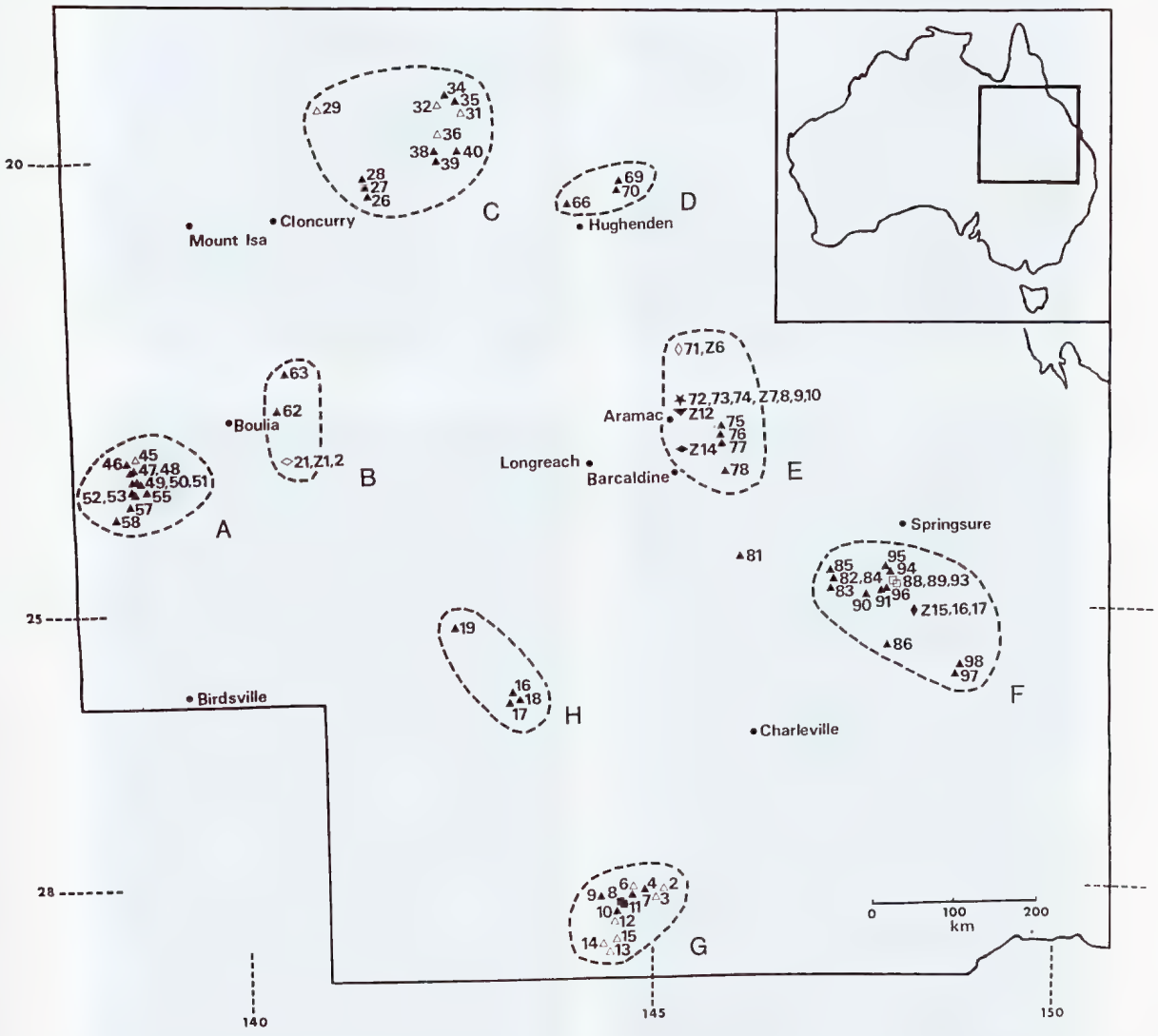


**Fig.1.** A map showing the locations of the springs sampled in Queensland and their hydrobiid fauna. The numbers are the field station numbers and correspond to those used in the text and in the Appendices. The dotted lines outline the main spring supergroups:- A, Mulligan River Supergroup; B, Springvale Supergroup; C, Flinders River Supergroup; D, Hughenden Supergroup; E, Barcaldine Supergroup; F, Springsure Supergroup; G, Eulo Supergroup; H, a group of non-artesian springs associated with Tertiary sediments and basalts. open triangle - extinct spring(s); closed triangle – active springs lacking hydrobiids; closed square – *J. eulo*; open horizontal diamond – *J. isolata*; open vertical diamond – *J. colmani* ; closed vertical diamond – *J. carnarvonensis*; open square – *J. exigua*; closed inverted traingle – *J. zeidlerorum*; closed horizontal diamond – *J. coreena*; closed star – Edgbaston species (*J. edgbastonensis*, *J. corrugata*, *J. acuminata*, *J. pallida*, *J. jesswisae* and *J.* sp.)

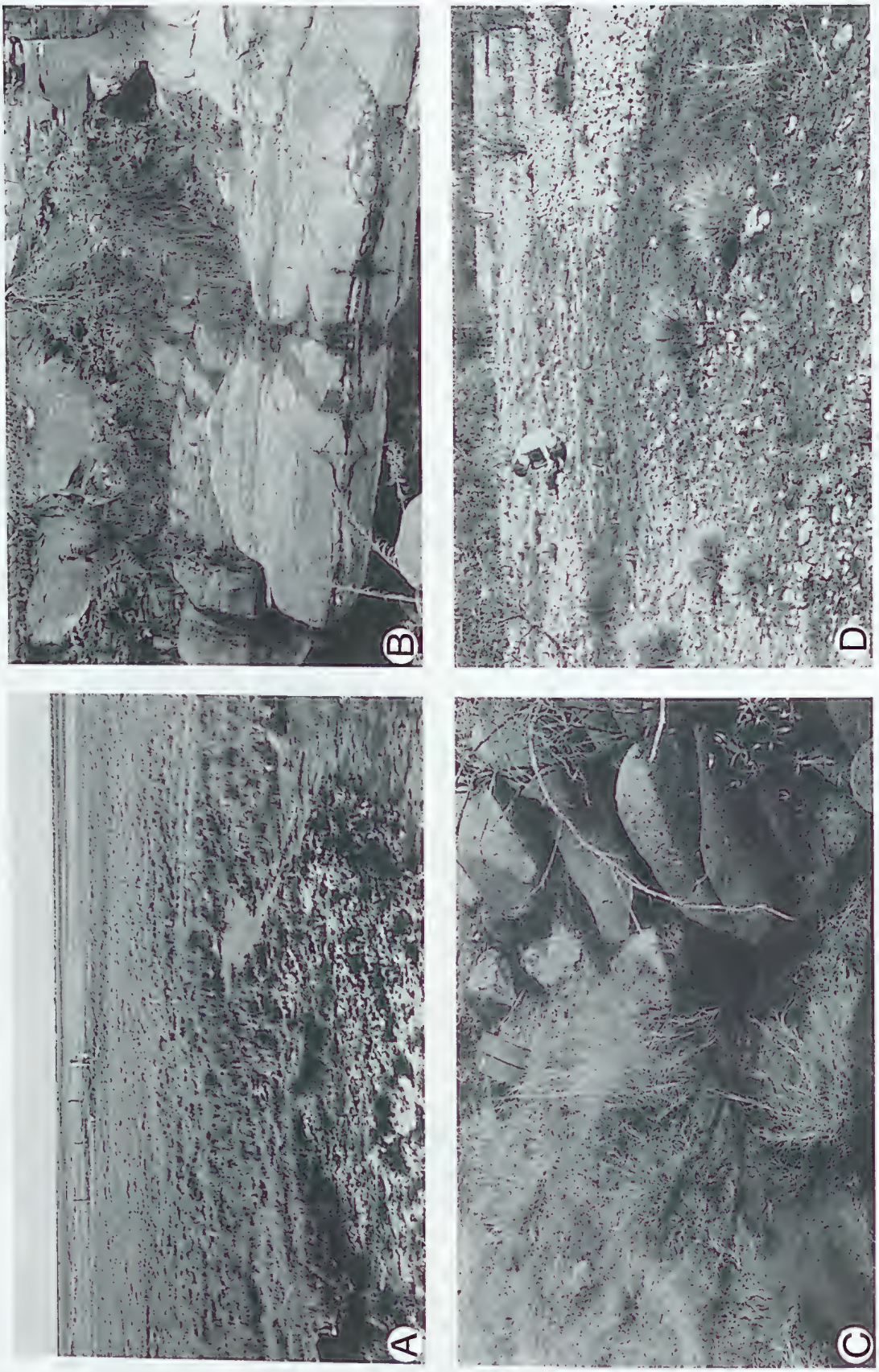


**Fig.2.** Some of the springs containing hydrobiids. A, Elizabeth Springs, near Springvale (Stn 21), photo W.F. Ponder (locality for *J. isolata*); B, Carnarvon Gorge National Park, springs at the beginning of Kooraminya Gorge (Stn Z16), photo W. Zeidler (locality for *J. carnarvonensis*); C, "Rocky Springs", near Eulo (Stn 11), photo W.F. Ponder (locality for *J. eulo*); D, spring at Tunga Bore, near Eulo (Stn 8), photo W.F. Ponder (locality for *J. eulo*).

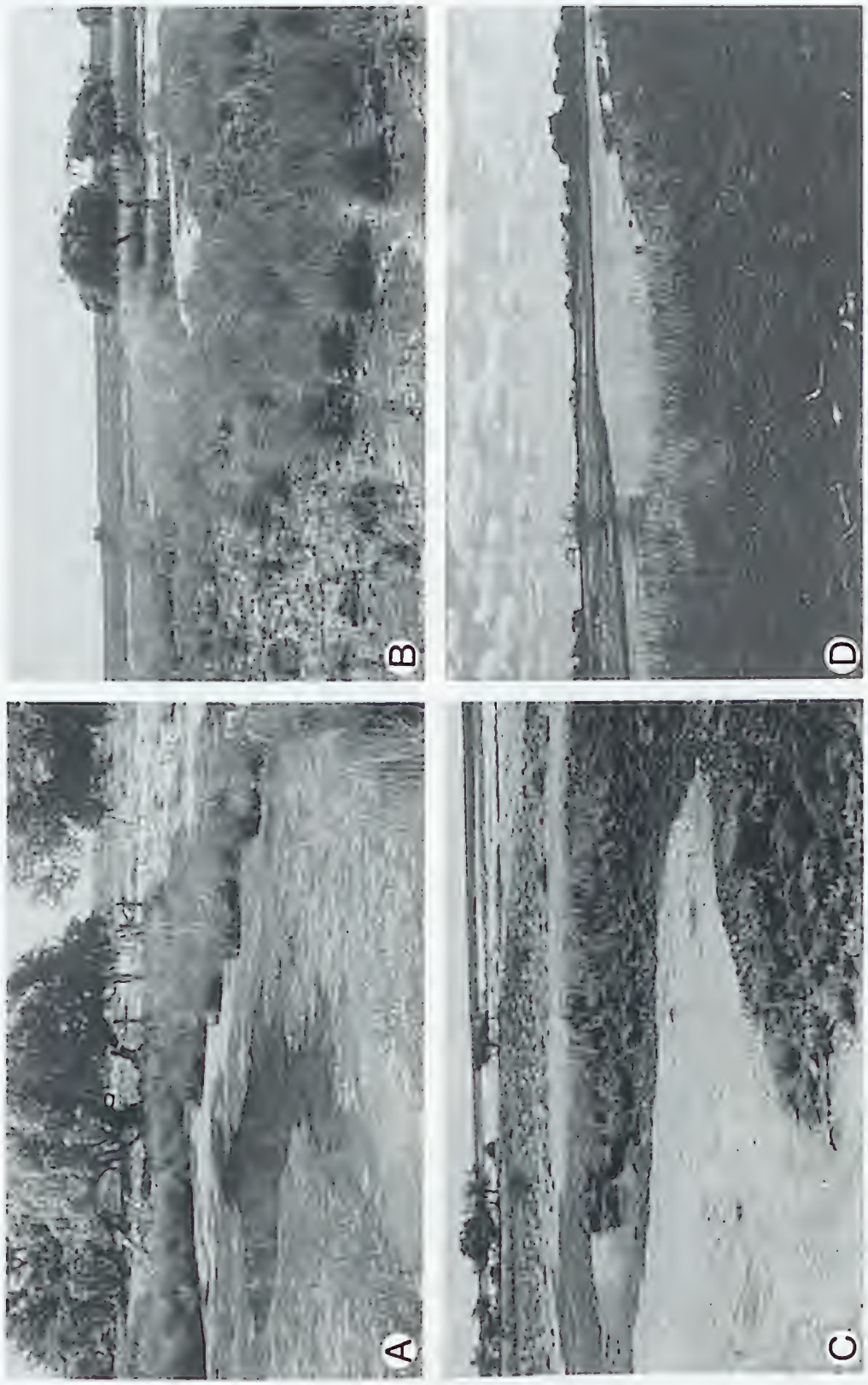


**Fig.3.** Some of the Edgbaston springs containing hydrobiids. A, the upper part of the outflow of "Big Spring" (Stn 73), photo W.F. Ponder; B, lower outflow of "Big Spring" (Stn 73), photo W.F. Ponder; C, small spring in Edgbaston group (Stn Z10), photo W. Zeidler; D, spring near Edgbaston group (Stn Z12), photo W. Zeidler (locality for *J. zeidlerorum*).

and the animal transfered to 70% ethanol. The structure required for examination was then carefully removed under a stereoscopic dissecting microscope. The specimens were then dehydrated through a series of acetone baths of increasing concentration (70%-100%) with 20 minutes in each bath and 20 seconds of ultrasound in an attempt to remove mucus residues. Critical point drying was done in an Emscope CPD750 at the School of Biological Sciences, Macquarie University. The dried specimens were mounted on aluminium stubs using electroconductive glue for SEM scanning. Most female genitalia were not used further because of lack of success in getting good results.

Because species could be readily discriminated using shell characters, anatomical investigation of each species was limited to a minimum of two individuals of each sex of each species. If differences were found between the first two individuals additional specimens were examined. A preliminary examination revealed several easily scored characters that assisted in discriminating the species (see Table 1). Dissections were carried out in a mixture of Bouin's fluid and water on a black wax background. Three to four specimens of each sex of eight species were serially sectioned and stained with Mallory's triple stain. These sections were used to confirm some of the observations made using gross dissection.

The radulae of a few individuals of each species were removed using KOH, washed with distilled water and mounted for photographing with a scanning electron microscope (SEM). The radular characters listed in Table 1 were scored from examination of the SEM photos.

All characters (see Table 1 for a full list) were entered into a computer file for use with the taxonomy package DELTA (Dallwitz & Paine, 1986). The output was used as the basis for the descriptions used in this paper. It also generated the initial data file used in the phylogenetic analyses. This was refined to produce the list of characters in Table 2 which were used in the final analysis.

The full range of measurements of several characters are given in the description of the shells and opercula, as well as the means for males (M) and females (F) for those characters. Means are also given in Table 3, in addition to standard deviations.

*Phenetic analysis.* Quantifiable evidence of differences in shell characters between the initially defined taxa were obtained by the use of multivariate statistics [discriminate analysis, using the statistical package BIOSTAT (Pimentel & Smith, 1986)]. The characters shell length, shell width, aperture length, body whorl length, convexity, width of umbilicus, protoconch diameter, and number of teleoconch whorls were used in this analysis. Those taxa that were not well discriminated were identified and statistical comparisons (t-test) between similar species pairs were carried out, using shell and opercular measurements (pooled sexes), with the statistical package SYSTAT (Wilkinson, 1987). Sexual dimorphism in shell size was also tested for using t-tests on shell length and width.

*Phylogenetic analysis.* The phylogenetic package PAUP (Swofford, 1985) was used to construct phylogenetic trees using the genus *Tatea* as an outgroup to root the trees and including the genera *Fluvidona* and *Fonscochlea* (with its subgenus *Wolfgangia*). *Fluvidona* is a freshwater genus widespread in south-eastern Australia and shares many characters with *Jardinella*. *Fonscochlea* is also morphologically similar to *Jardinella* and is found in artesian springs in South Australia (Ponder *et al.*, 1989). The options MULPARS and SWAP=GLOBAL were used. Shell characters and other characters judged to show considerable homoplasy were excluded from the analysis.

Not all of the characters used in generating the descriptions were appropriate for use in phylogenetic analysis. They must have at least two states, each state should exist in at least two taxa and should be, as far as can be determined, homologous. Homology is difficult to identify with certainty because of homoplasy and no guarantee can be given for any character state. After analysis convergences can be identified, but a meaningful result is always dependent on the relative proportion of correctly identified homologous apomorphies.

Characters were chosen for use in this analysis from the characters used in the descriptions (indicated by an asterisk in Table 1; listed in more detail in Table 2). Characters were excluded that were considered to exhibit a high level of homoplasy or which could not be readily assigned to discrete character states. No shell characters are used, with the exception of the number of protoconch whorls, and this was included because of the choice of outgroup. *Tatea* T.Woods, 1879 was chosen as the outgroup because this estuarine genus appears to be one of the most plesiomorphic of the group of genera to which *Jardinella* belongs. It is similar anatomically, including the reproductive systems, to species of *Hydrobia*, another estuarine group that is considered to be primitive within the family (Ponder, 1988, and unpublished observations). The characters listed for *Tatea* are based on dissections and SEM investigations of species of *Tatea* from Tasmania and New South Wales, including topotypes of the type species.

Museum abbreviations used are: AMS – Australian Museum Sydney; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide.

## Results

## Systematics

### Hydrobiidae

#### *Jardinella* Iredale & Whitley

*Jardinella* Iredale & Whitley, 1938: 67.

**Type species.** *Petterdiana thaanumi* Pilsbry, 1900 (by original designation).

**Diagnosis.** Shell variable in shape (depressed

trochoid to elongate conic), with evenly convex whorls, umbilicate to nonumbilicate, usually lacking true sculpture but rarely (in one species) with axial growth lines thickened as riblets. Growth lines and outer lip of aperture prosocline; periphery of body whorl evenly convex. Protoconch of 1.2-1.5 whorls, sculptured with minute pits.

Operculum yellow to reddish brown, with eccentric nucleus, inner surface with or without white smear, sometimes with small horny lump on inner surface near nucleus, lacking pegs.

Radula taenioglossan, each central tooth typically with 2 pairs of basal processes, innermost larger; sometimes with 1 or 3 pairs. Cutting edge formula (2-5):1:(2-5). Each lateral tooth with narrow, straight, short to long outer flange (ratio of cutting edge to length of flange 1.3-2.6); cutting edge formula (2-4):1:(3-5). Marginal teeth with numerous, small, sharp cusps, those on inner marginal teeth larger.

Head-foot pigmented with grey to varying extent, usually with a dark grey patch behind eyes. Cephalic tentacles usually bear 1-3 longitudinal tracts of cilia ventrally, some species with 1 tract dorsally, only on right side in some. No pallial tentacle(s).

*Pallial cavity* (Figs 4A,B, 5D–F): ctenidium (c) well developed, with broadly triangular filaments, osphradium

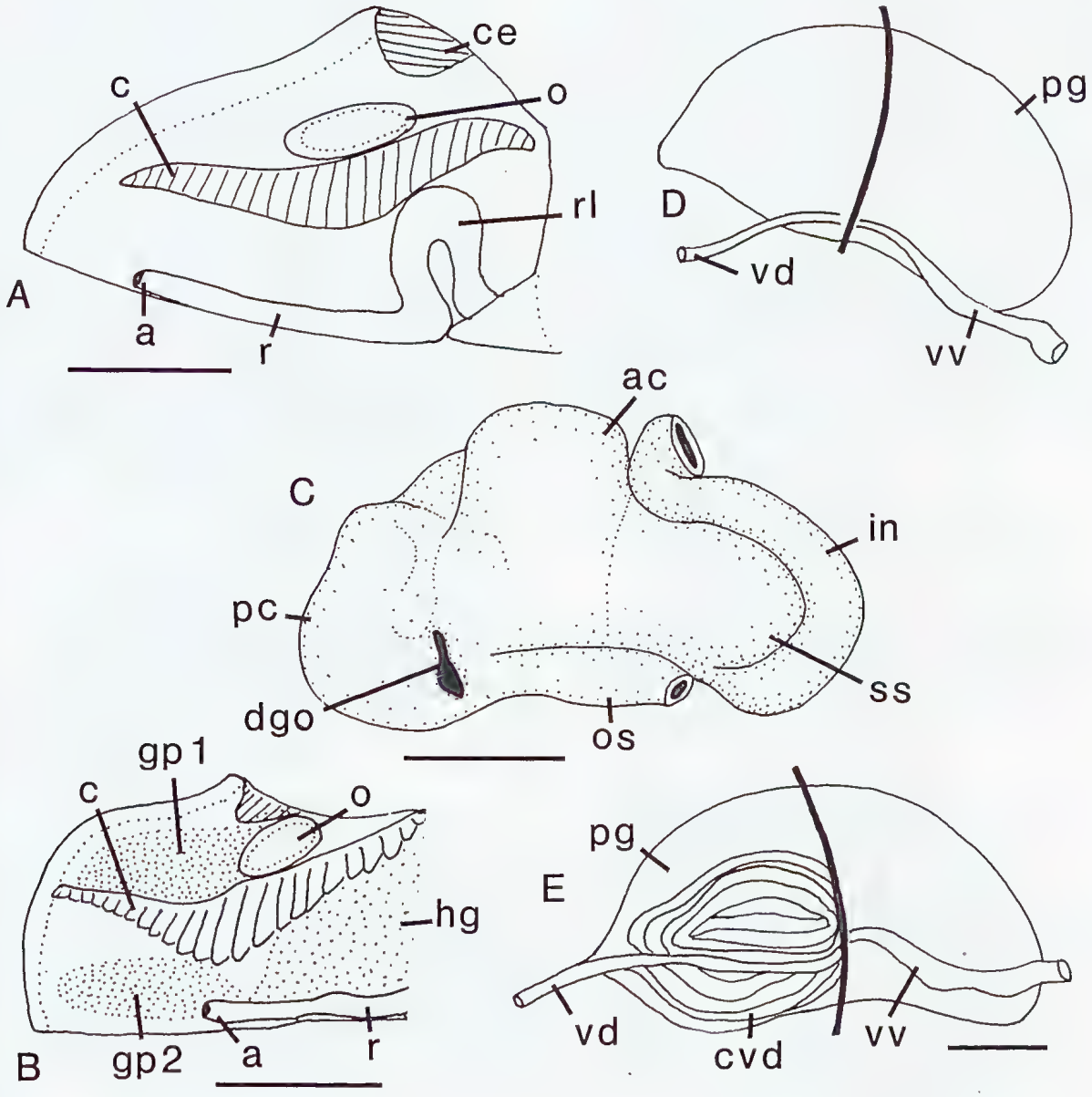


**Fig.4.** A,B, the inside of the pallial roof of *Jardinella carnarvonensis* (A) and *J. acuminata* (B) showing the main pallial structures. C, stomach of *J. edgbastonensis*. D,E, prostate glands of *Jardinella* sp. (D) (generalised and shows the prostate form for the majority of species) and *J. exigua* (E). The heavy black line represents the posterior wall of the pallial cavity. a – anus; ac – anterior chamber; c – ctenidium; ce – cut area; cvd – coiled pallial vas deferens; dgo – digestive gland opening; gp1 – glandular pad to left of ctenidium; gp2 – glandular pad near anus; hg – hypobranchial gland; in – intestine; o – osphradium; os – oesophagus; pc – posterior chamber; pg – prostate gland; r – rectum; rl – rectal loop; ss – style sac; vd – pallial vas deferens; vv – visceral vas deferens. Scales:- A,B,C – 0.5 mm, E – 0.1 mm.

(o) elongately oval, situated alongside posterior half of ctenidium, not extending to posteriormost part of ctenidium. Hypobranchial gland (hg) very well developed to absent, restricted to posterior part of pallial cavity when present. Glandular pads near anus (gp2) and left of ctenidium (gp1) present in 2 species. Renal organ abuts against posterior end of pallial cavity and, in some species, extends dorsally a little into pallial roof. Stomach (Fig. 4C) short, stomach/style sac ratio 0.9-1.9, with well-developed posterior (pc) and anterior (ac) chambers, the anterior chamber larger. Digestive gland opening (dgo) a simple slit above the oesophageal opening.

Male with penis situated on right side of neck and curled back into pallial cavity when at rest. Penis with broad basal portion, with surface concentrically folded when at rest, and smooth, often cuticularised, distal portion which, in some species, forms papilla. Simple, flattened, non-glandular, often pigmented lobe(s) present on distal part of penis in some species. Penial duct undulating in basal part of penis, more or less straight in distal part. Pallial vas deferens narrow, simple tube lying just below pallial floor, typically with multiple loops in section anterior to prostate, sometimes coiled over pallial part of prostate (Fig. 4E, cvd). Prostate gland (Fig. 4D,E, pg) about half to one third in pallial roof, with visceral vas deferens entering gland just behind posterior pallial wall and pallial vas deferens emerging from gland just in front of posterior pallial wall. Seminal vesicle long and coiled, anteriorly on stomach and posteriorly lying beneath about first half whorl of testis.

Female with large yolky eggs. Pallial oviduct mainly large capsule gland, posterior albumen gland usually immediately behind posterior pallial wall. Ventral channel simple (Fig. 5F, vc) and with anterior pallial opening in few species but typically with large, muscular vestibule at least partly separated from capsule gland (Fig. 5D,E, v), some species with pallial opening set off on short papilla. Type species with pallial opening about one third length of capsule gland posterior to anterior end of capsule gland. Vestibule, when present, often with deeply folded walls internally (Fig. 5E) and used for (short term?) sperm storage. Coiled oviduct non-pigmented, thinly muscular, basically U-shaped, lying on inner (left) side of albumen gland, with additional folds in some species. Bursa copulatrix posterior to albumen gland, ovate, with duct emerging from anterior face and joining oviduct at variable points from just in front of seminal receptacle duct to posterior wall of pallial cavity. Bursa copulatrix missing in one species. Seminal receptacle small, thin walled, usually on anterior edge of bursa copulatrix, rarely more posteriorly located.

**Remarks.** The original introduction of this genus name barely meets the requirements of the code ["*Jardinella* (type *Petterdiana thaanumi* Pilsbry), a small globose freshwater rissoid, of unknown relationship"]. The genus is based on a species found in rivers and streams in the vicinity of Cairns, north-east Queensland. The type species shows the essential features exhibited by the species in the Queensland spring radiation described

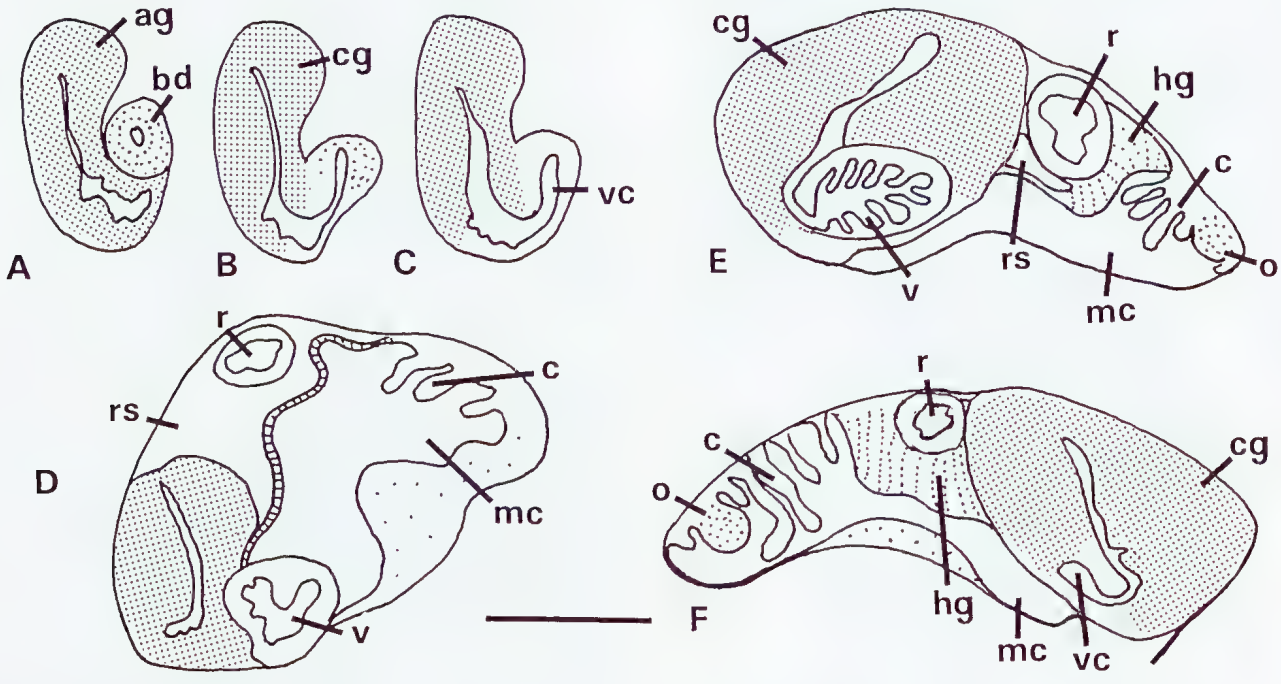


**Fig.5.** Sections of female pallial genital ducts and pallial cavities of species of *Jardinella*. A–D, *J. colmani*, Stn 71, A–C, sections through the anterior albumen gland (A) and posterior part of the capsule gland (B,C); D, section through the pallial cavity and the anterior part of the capsule gland; E, *J. jesswiseae*, Stn 73(A), section through the pallial cavity and capsule gland showing the vestibule; F, *J. acuminata*, section through the pallial cavity and middle part of the capsule gland. ag – albumen gland; bd – bursal duct; c – ctenidium; cg – capsule gland; hg – hypobranchial gland; mc – pallial cavity; o – osphradium; r – rectum; rs – rectal sinus; v – vestibule; vc – ventral channel. Scale:- 0.2 mm.

below, including a coiled pallial vas deferens, a smooth distal penis (lacking lobes), a white smear on the operculum and two pairs of basal cusps on the central teeth of the radula. Females lack a swollen anterior vestibule but the ventral channel is wide and internally thickened. This species is not dealt with in this paper but is treated in detail elsewhere (Ponder, in press).

*Jardinella* is distinguished from all other related genera in usually possessing two pairs of cusps on the central teeth of the radula and in never developing "calcareous" pegs on the operculum, although there is often a white smear. Some specimens of *Fonscochlea*, one of two described genera from South Australian artesian springs (Ponder *et al.*, 1989), resemble *Jardinella* in these characters but species of the former genus develop opercular pegs in most specimens of all but one species and even that species usually has rudimentary pegs. In addition, species of *Fonscochlea* have the osphradium very close to the posterior end of the ctenidium, not positioned in the third quarter (from the anterior end of the ctenidium) of the length as in species of *Jardinella*, and never develop a lobulate penis or coiled pallial vas deferens as is seen in most species of *Jardinella*. However, the major distinguishing autapomorphy of *Fonscochlea* is that females possess two equal-sized sperm sacs which lie alongside the posterior end of the albumen gland. The only other described hydrobiid genus from the South Australian mound springs is *Trochidrobia*. The species in that genus resemble the trochiform species of *Jardinella* in shell characters but differ in lacking a lobulate penis and coiled pallial vas deferens and in possessing only a single sperm sac (bursa copulatrix) in females. In addition, the opercular nucleus is located subcentrally in *Trochidrobia* and there is no trace of white material on the operculum. An undescribed genus, apparently related to *Jardinella*, from Dalhousie springs, South Australia (Ponder, 1989) differs from *Fonscochlea* and *Jardinella* in having only a single sperm sac (the bursa copulatrix). Species in that genus resemble those of *Jardinella* in lacking or having weak opercular pegs (as do a few taxa of *Fonscochlea*).

Another related genus, *Fluvidona* Iredale, 1937, is widespread in south-eastern Australia. It has been known under several names in recent literature including *Pupiphryx* Iredale, 1943 and *Rivisessor* Iredale, 1943 (used by Smith & Kershaw, 1979) and *Hemistomia* (as used by Ponder, 1982). Another synonym is *Angrobia* Iredale, 1943, and *Posticobia* Iredale, 1943 is at best a subgenus. The New Zealand genus *Potamopyrgus* Stimpson, 1865 and the south-western Pacific genus *Fluviopupa* Pilsbry, 1911 are also related. *Fluvidona* differs from *Jardinella* in having three or more pairs of basal cusps and in never developing penial lobes, a coiled pallial vas deferens or a vaginal papilla. In addition, most species of *Fluvidona* have well-developed white pegs on the inner surface of the operculum. Species of *Potamopyrgus* (see Winterbourn, 1970) resemble species of *Fluvidona* in both radular characters and anatomically, but never develop pegs on the operculum, although they often have a white smear. Some species of *Potamopyrgus* brood embryos in the modified capsule gland. *Fluviopupa* species (see Ponder, 1982) have an accessory lobe on the penis and do not brood but otherwise resemble *Potamopyrgus*.

The genera listed above (with the possible exception of *Trochidrobia*) form a clade within the Hydrobiidae for which the subfamilial name Tateinae Thiele, 1925 is available (see Ponder & Warén (1988) for additional synonyms). No Australasian genera that fall outside this group have white material on the inner surface of the operculum. The origin and relationships of *Jardinella* are further discussed in the phylogenetic section below.

There is a considerable amount of diversity in the shell and anatomical characters in the group of species that we have included in *Jardinella*, although further subdivision may prove to be warranted when additional information, particularly biochemical data, becomes available. The considerable geographic spread of the genus and the divergence in anatomical and shell morphology, are in accord with the idea that it is the remnants of a much larger group of at least mid-Tertiary origin (see Discussion).

The species are described below in the four geographic areas in which they occur (see Fig. 1). These are:-

1. *Barcaldine Supergroup*:– springs on the eastern edge of the Basin north east of Longreach, including Edgbaston Springs.
2. *Springsure Supergroup*:– springs on the eastern side of the Basin west of Rolleston.
3. *Springvale Supergroup*:– springs on the western edge of the Basin south east of Boulia.
4. *Eulo Supergroup*:– springs on the southern side of the Basin west of Eulo.

## Species from the Barcaldine Supergroup

### *Jardinella edgbastonensis* n.sp.

**Localities.** Stn 72, unnamed spring 2.3 km north-east of "Edgbaston" homestead, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaburra 338 486. WFP and PHC, 26 Sept. 1984. Large spring, with outflow about 220 m, on open plain. A – general; C – on sheep skull; E – edge of outflow 50 m from head; F – 20 m from end of outflow. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WFP and PHC, 26 Sept. 1984. Large spring, with outflow about 170 m. B – lower part of outflow; C – small seep. Stn Z7, unnamed spring about 2.4 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°42'45"S 145°25'25"E. Muttaburra 338 487. WZ, 3 May 1988. No mound but extensive seepage.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 72(A) C.156738 (holotype), C.156739 (250 paratypes), Stn 72(C) C.156744 (11 paratypes), Stn 72(E) C.156741 (160 paratypes), Stn 72(F) C.156740 (460 paratypes), Stn 73(B) C.156742 (15 paratypes), Stn 73(C)

C.156743 (120 paratypes), SAM Stn Z7 D.18524 (4 paratypes), Stn 72(F) D.18525 (20 paratypes), QM Stn 72(F), MO.20075 (5 paratypes).

**Diagnosis.** Shell trochiform, of medium size (up to 3.2 mm), smooth or with weak, rounded axial ribs, umbilicate. Penis with long, tapering distal portion, pigmented distally. Pallial oviduct with wide vestibule and ventral opening anterior to capsule gland.

**Description.** *Shell* (Figs 6A, 7): trochiform, of medium size, 2.47-3.22 mm in length [mean 2.80 (M), 2.98 (F)]; 2.36-2.86 mm in width [mean 2.43 (M), 2.58 (F)]; sexually dimorphic in size (P less than 0.05); of medium thickness, translucent white, with indistinct, transparent periostracum. Spire angle 75.49-92.92° [mean 83.17 (M), 84.47 (F)]. Protoconch (Fig. 7A,B) of 1.2-1.4 whorls [mean 1.31 (M), 1.35 (F)]. Teleoconch of 2.75-3.2 convex whorls [mean 2.99 (M), 3.03 (F)]. Convexity ratio 0.19-0.31 [mean 0.26 (M & F)]. Teleoconch sculpture of faint, prosocline growth lines sometimes strengthened to form rounded riblets (Fig. 7D). Aperture length/shell length ratio 0.51-0.6 [mean 0.57 (M), 0.56 (F)]. Inner lip of medium thickness, of medium width.

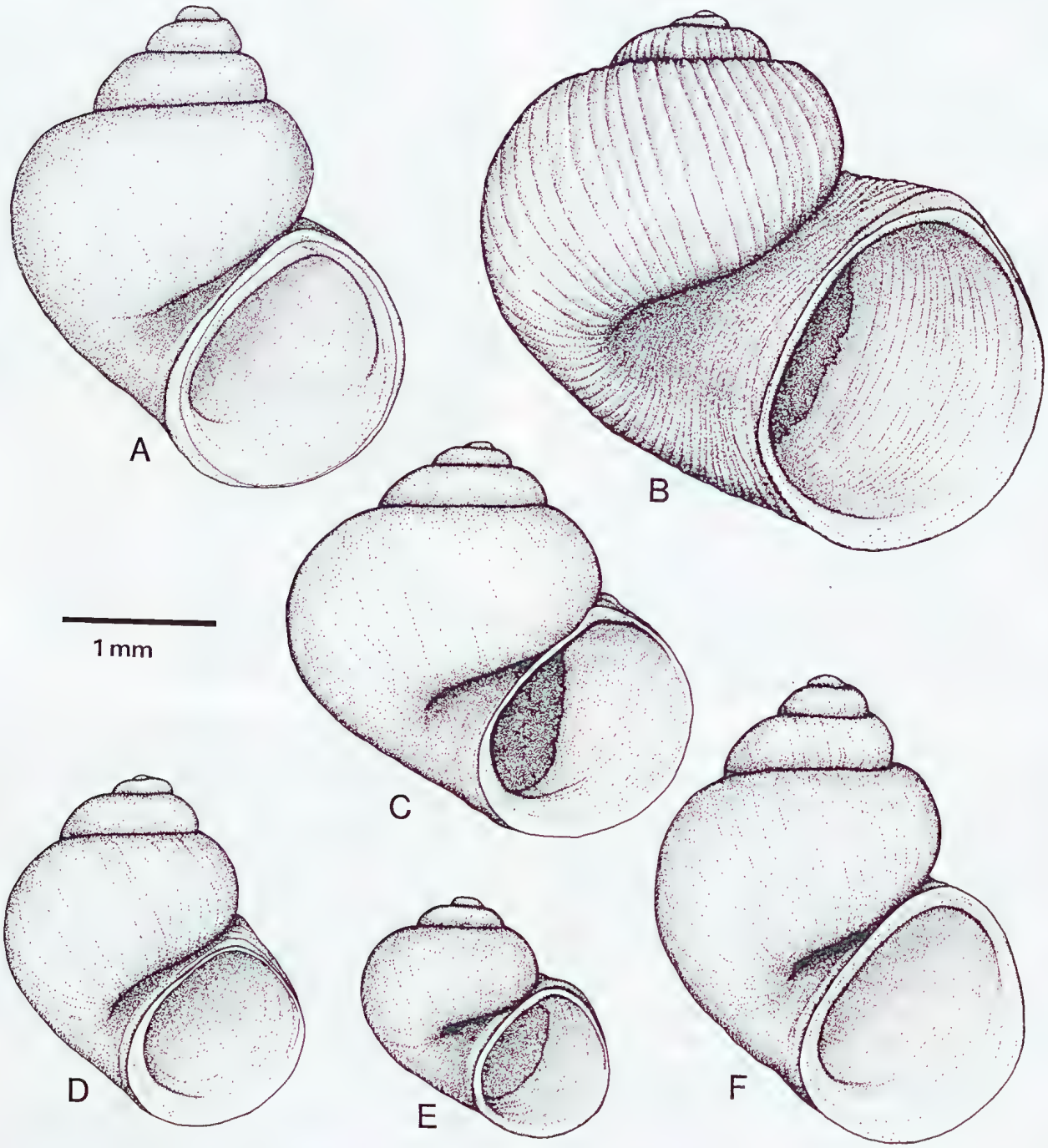


**Fig.6.** Shells of holotypes of species of *Jardinella*. A – *J. edgbastonensis*; B – *J. corrugata*; C – *J. eulo*; D – *J. carnarvonensis*; E – *J. exigua*; F – *J. coreena*.

Outer lip prosocline, angle 14.31-26.27° [mean 20.33 (M), 22.18 (F)]. Umbilicus of medium width [0.27-0.43 mm; mean 0.33 (M), 0.35 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 3.08 mm, width 2.54 mm, length of aperture 1.68 mm, number of teleoconch whorls 3.10.

*Operculum* (Fig. 8A): thin, pale yellow, 1.21-1.61 mm in length [mean 1.36 (M), 1.45 (F)]. With or without white smear up to 0.93 mm in length [mean 0.15 (M), 0.24 (F)]. Ratio of opercular length to position of nucleus 2.94-3.55 [mean 3.24 (M), 3.30 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 8B,C): each central tooth with 2-3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.4-1.5; 2 (rarely 3) pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula (2-3).1.4; ratio of length of primary cusp/length of adjacent outer cusps 1.6-1.8; with small basal bulge; outer shaft 1.6 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Fig. 9A) oval in section, with no dorsal ciliated bands present; 2 distinct ciliated bands along most of ventral surface. Snout dark grey to black; anterior end unpigmented; dorsal sides of cephalic tentacles pale to dark grey with unpigmented patch either around eye or anterior to eye; sides of foot and opercular lobe pale to dark grey. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 27-31 filaments;

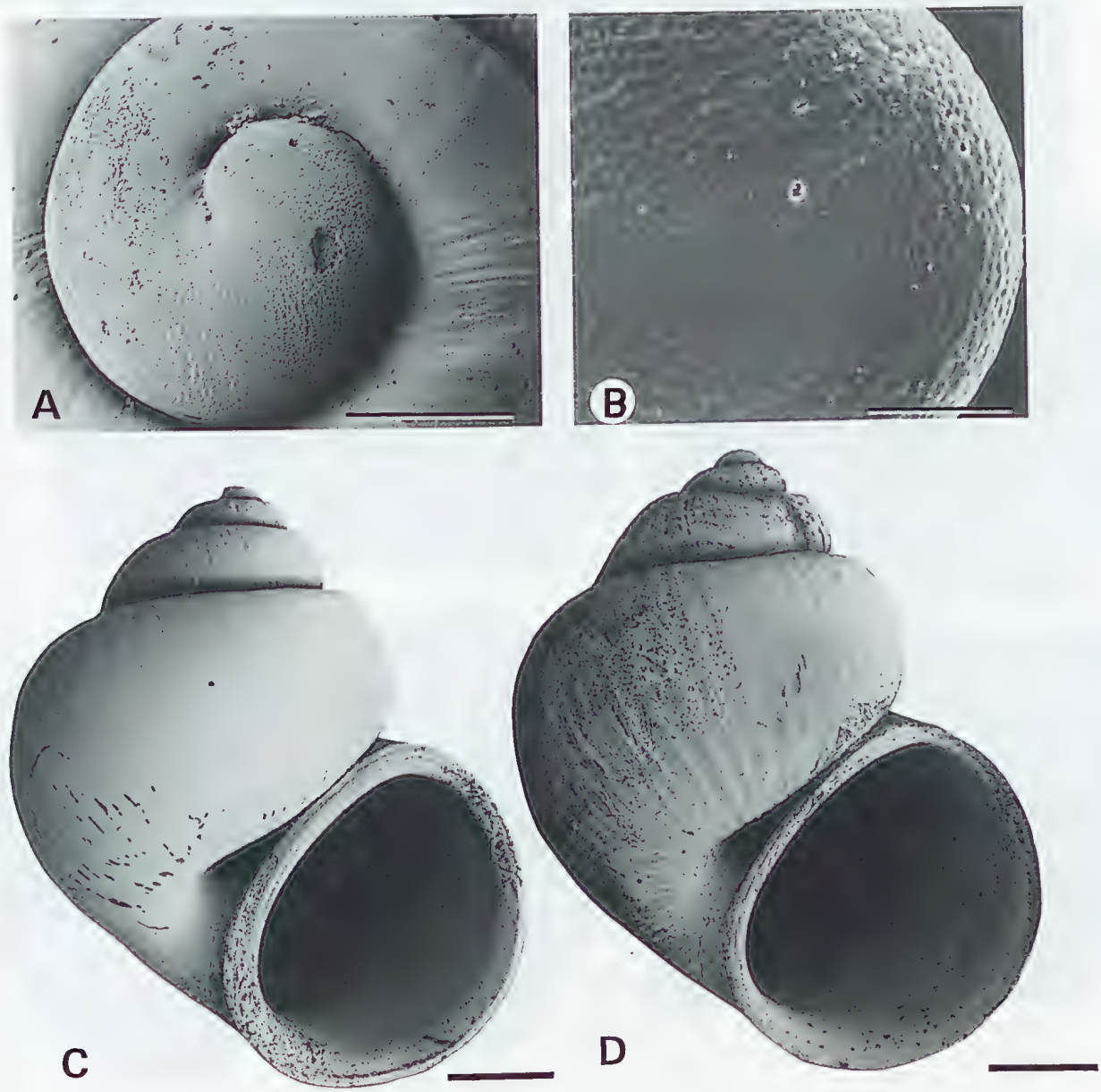


**Fig.7.** *Jardinella edgbastonensis* n.sp., Stn 72(F), shell. A, dorsal view of protoconch; B, protoconch microsculpture; C, D, shells showing variation in sculpture. Scales:- A – 0.1 mm, B – 0.02 mm, C,D – 0.5 mm.

apex on right or towards centre. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with slight arch, anus with intermediate position relative to mantle edge. Kidney either not extending forward into pallial roof or extends forward slightly.

*Male reproductive system* (Figs 10A, 11A,B): penial lobe(s) absent; distal end of penis tapering; with broad grey band at proximal end of terminal portion; remainder unpigmented except for grey basal fold. Vas deferens with several loops/coils anterior to prostate gland

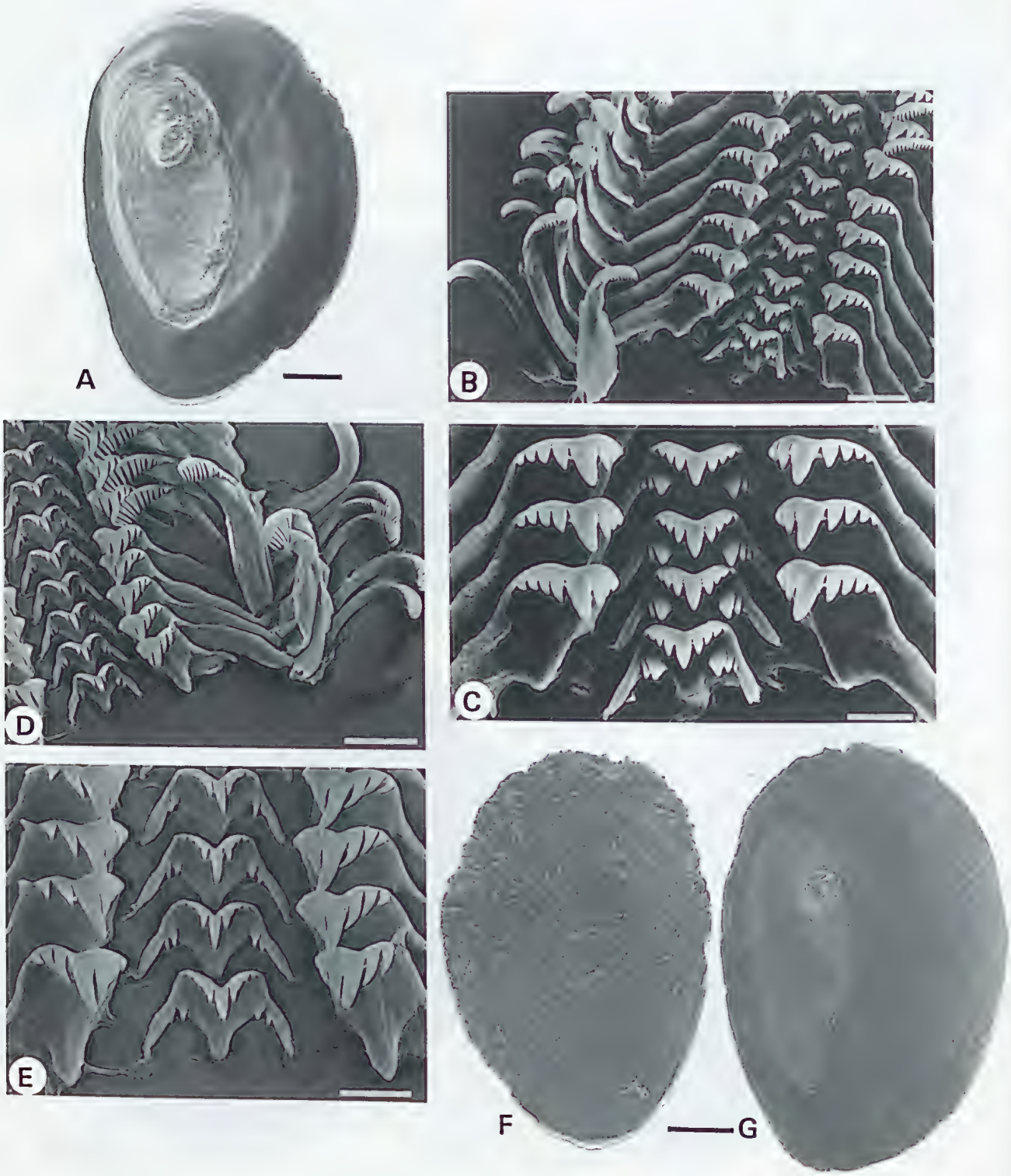


**Fig.8.** *Jardinella edgbastonensis* n.sp. and *Jardinella corrugata* n.sp., opercula and radulae. A–C, *J. edgbastonensis*, Stn 72(F); A, inner view of operculum; B,C, radula, C showing detail of central and lateral teeth. D–G. *J. corrugata*, Stn 73(C); D, E, radula, E showing detail of central and lateral teeth; F, G, outer (F) and inner (G) sides of operculum. Scales:- A,F,G – 0.250 mm, B,D – 0.02 mm, C,E – 0.01 mm.

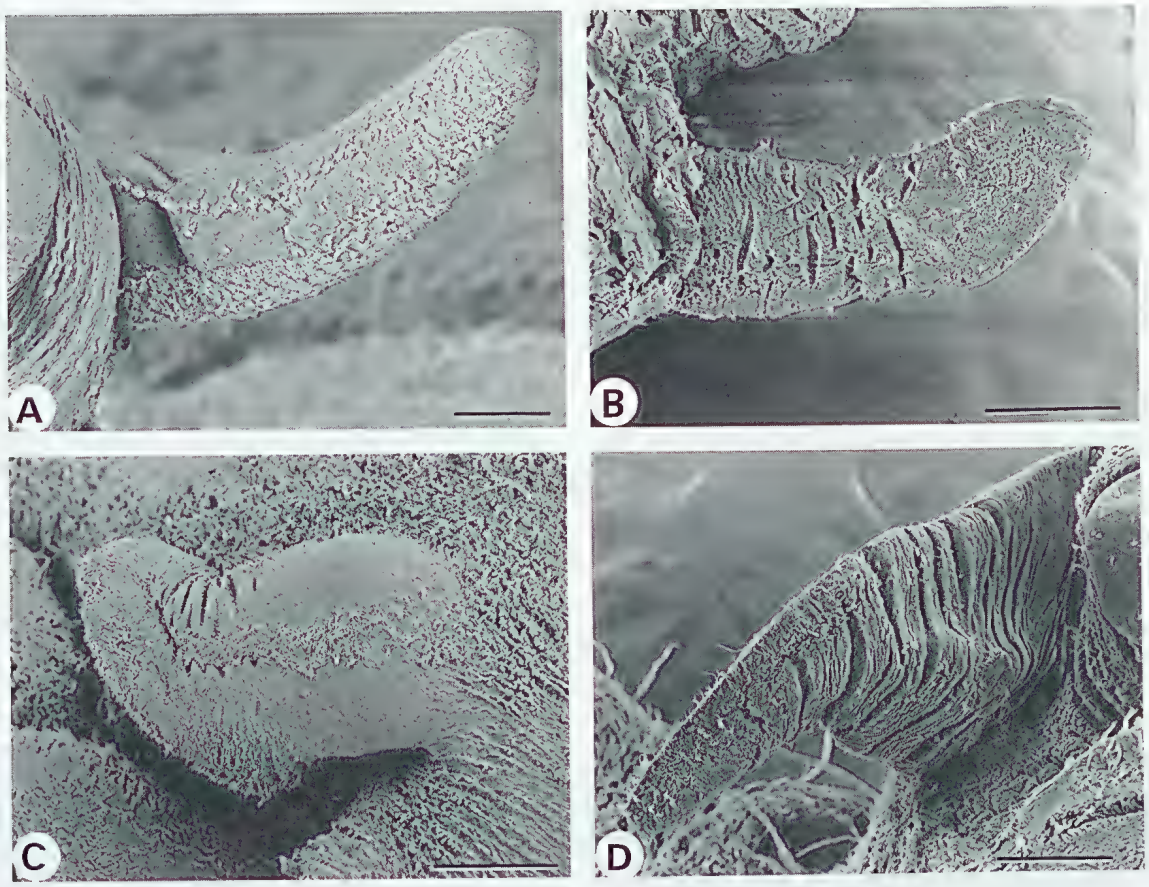


**Fig.9.** Scanning electron micrographs of critically point dried cephalic tentacles of species of *Jardinella*. A, *J. edgbastonensis*, Stn 72(A), ventral view of left tentacle; B, *J. exigua*, Stn 93, ventral view of left tentacle; C, *J. corrugata*, Stn Z9(A), dorsal view of right tentacle; D, *J. carnarvonensis*, Stn Z15, ventral view of right tentacle. Scales:- A,C – 0.1 mm, B,D – 0.05 mm.

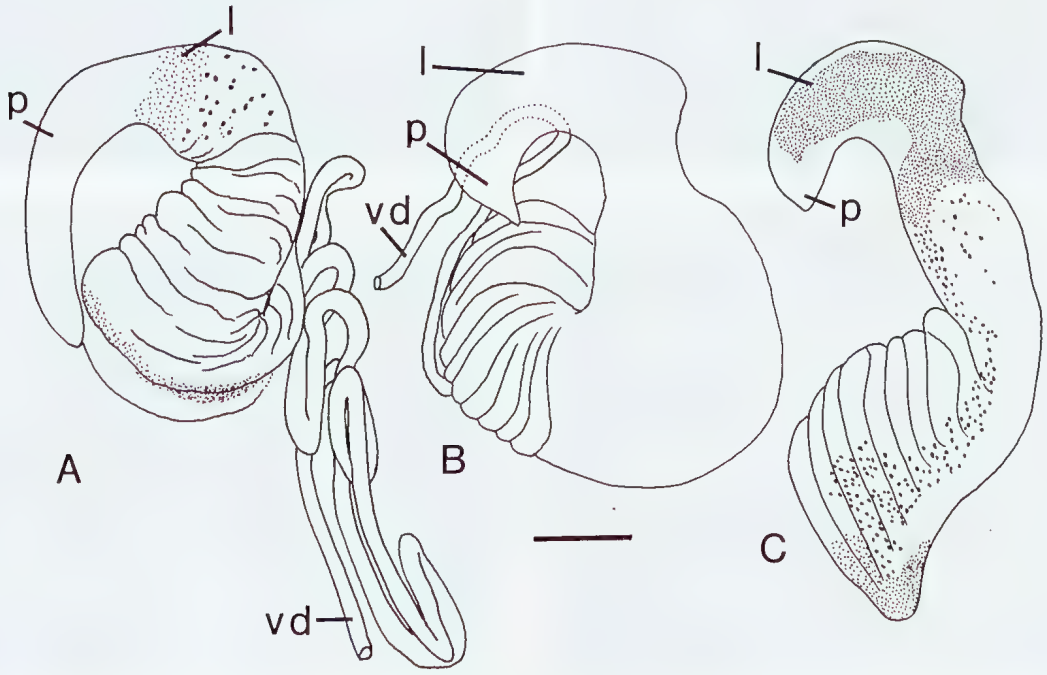


**Fig.10.** Penes of species of *Jardinella*. A. *J. edgbastonensis*, Stn 72(A); B, *J. coreena*, Stn Z14; C, *J. corrugata*, Stn Z9(A). The stipple indicates pigmentation. l – penial lobe or homologous area; p – penial papilla; vd – pallial vas deferens. Scale:- 0.25 mm.

(Fig. 10A, vd).

*Female reproductive system* (Fig. 12A,B): pallial oviduct with ventral channel modified as wide, muscular vestibule, duct extended anterior to capsule gland as ventrally located papilla. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix, which lies posterior - posteroventral to, and is smaller than, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

**Remarks.** This species is anatomically and conchologically the most similar of the spring species to the coastal type species of the genus. The rather large (for the genus) trochiform shell somewhat resembles that of two other spring species, *J. corrugata* n.sp. and *J. coreena* n.sp. from which it is distinguished in the following descriptions of these two species. It lives in the Edgbaston Springs along with five other species (Table 4) but appears to prefer the shallow, marshy outflows where it occurs together with *J. corrugata* in Stn 73 (*J. corrugata* was not found in Stn 72).

**Etymology.** Named for Edgbaston Station, north-east of Aramac.

### *Jardinella corrugata* n.sp.

**Localities.** Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WFP and PHC, 26 Sept. 1984. Large spring, with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain (= Stn 73). Stn Z10, unnamed spring about 3.3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'30"S 145°25'40"E. Muttaburra 339 483. WZ, 4 May 1988.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn Z9(B) C.156769 (holotype), Stn 73(B) C.156770 (40 paratypes), Stn 73(C) C.156771 (70 paratypes), SAM

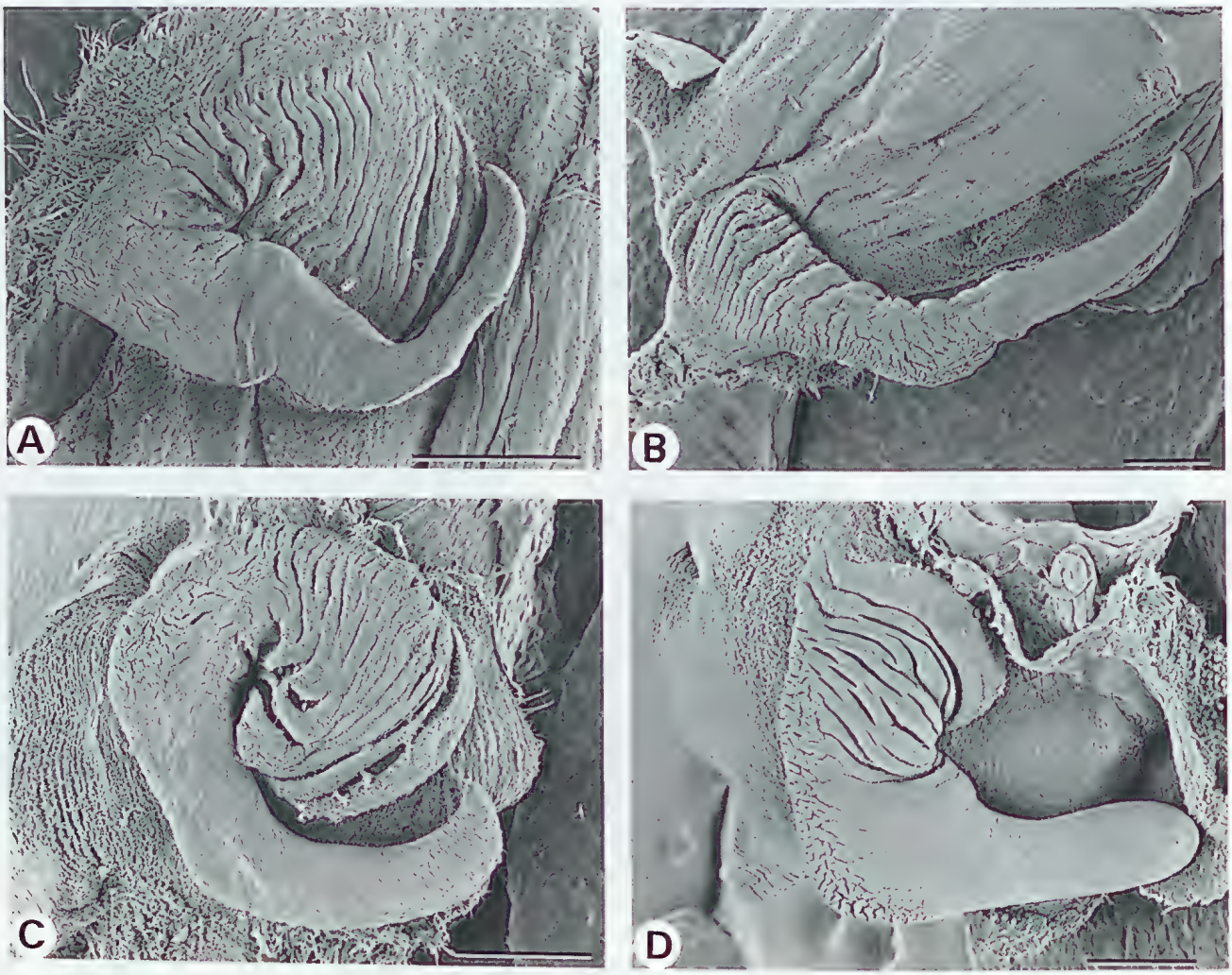


**Fig.11.** Scanning electron micrographs of critically point dried penes of species of *Jardinella*. A,B, *J. edgbastonensis*, Stn 72(A); C, *J. coreena*, Stn Z14; D, *J. corrugata*, Stn Z9(A). Scales:- 0.2 mm.

Stn Z9(A) D.18526 (60+ paratypes), Stn Z9(B) D.18527 (60+ paratypes), Stn Z10 D.18528 (60+ paratypes), Stn Z10 C.157421 (3 paratypes), QM Stn 73(C) MO.20076 (3 paratypes).

**Diagnosis.** Shell trochiform, large for genus (up to 4 mm in length), sculptured with weak, sharp riblets, widely umbilicate. Penis pigmented, with flattened distal lobe. Pallial oviduct with very wide, laterally located vestibule and terminal, laterally located opening.

**Description.** *Shell* (Figs 6B, 13): trochiform, large, 3.46-4.06 mm in length [mean 3.66 (M), 3.73 (F)]; 3.22-3.69 mm in width [mean 3.44 (M), 3.49 (F)]; not sexually dimorphic in size (P greater than 0.5); of medium thickness, translucent white, with indistinct, transparent periostracum. Spire angle 85.96-102.39° [mean 91.05 (M), 93.81 (F)]. Protoconch (Fig. 13D,E) of 1.25-1.35 whorls [mean 1.28 (M), 1.26 (F)]. Teleoconch of 2.7-2.9 convex whorls [mean 2.80 (M), 2.79 (F)]. Convexity ratio 0.28-0.38 [mean 0.32 (M), 0.33 (F)]. Teleoconch sculpture of faint to distinct, sharp axial riblets, and prosocline growth lines. Aperture length/shell length ratio 0.52-0.66 [mean 0.63 (M), 0.60 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 19.28-31.88° [mean 23.68 (M), 24.72 (F)]. Umbilicus wide [1-1.29 mm in width; mean 1.07 (M), 1.16 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 3.49 mm, width 3.65 mm, length of aperture 2.33 mm, number of teleoconch whorls 2.70.

*Operculum* (Fig. 8F,G): thin, very pale yellow, 1.77-2.11 mm in length [mean 1.93 (M), 1.97 (F)]. With white smear 0.01-0.71 mm in length [mean 0.33 (M), 0.42 (F)]. Ratio of opercular length to position of nucleus 2.47-3.71 [mean 3.22 (M), 3.32 (F)].

*Dimensions:* see Table 3.

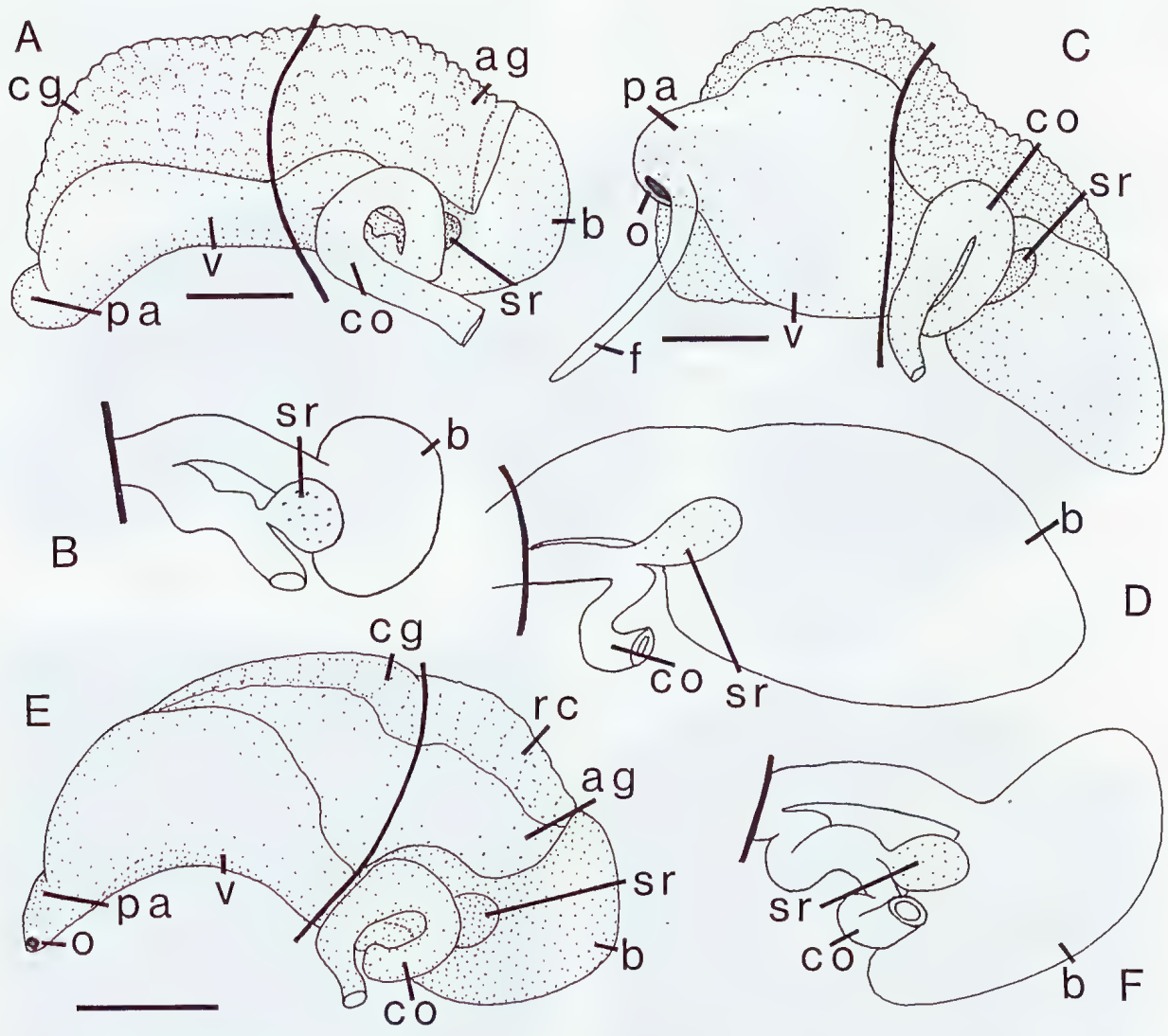


**Fig.12.** Female genitalia of species of *Jardinella*. A,B, *J. edgbastonensis*, Stn 72(A); C,D, *J. corrugata*, Stn Z9(A); E,F, *J. coreena*, Stn Z14. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; f – fold; o – oviduct opening; pa – papilla with oviduct opening; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule. Scales:- 0.25 mm.

*Radula* (Fig. 8D,E): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.3-1.6; 2 pairs of basal denticles; dorsal edge concave to dorsal edge inverted U-shaped; basal process long, tongue shaped; does not protrude beyond basal margin. Each lateral tooth with cusp formula (3-4).1.(3-4); ratio of length of primary cusp/length of adjacent outer cusps 1.6-1.9; with well-developed basal bulge; outer shaft 1.7-2 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Fig. 9C) triangular in section, with dorsal ciliated band present on right tentacle only; 3 ciliated bands along most of ventral surface. Head and foot black to dark grey, sometimes with thin, mid-dorsal unpigmented line on cephalic tentacles. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 26-28 filaments; apex on right, or towards centre. Osphradium near middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with slight arch, anus near mantle edge. Kidney not extending forward into pallial roof.

*Male reproductive system* (Figs 10C, 11D): penial lobe distal; distal end of penis blunt; penis with black zone at proximal end of terminal portion; small black spots proximal to this; proximal part of base partially black. Vas deferens with few loops/coils anterior to prostate gland.

*Female reproductive system* (Fig. 12C,D): pallial oviduct with ventral channel modified as wide, laterally located, muscular vestibule, duct extended as laterally placed papilla protruding beyond blunt anterior edge of capsule gland. Thin fold of tissue runs from oviduct opening anteriorly. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate to subtriangular bursa copulatrix which is about equal in size to albumen gland and posterior to it. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

**Remarks.** This species is generally similar to *J. edgbastonensis* n.sp. in size and shape but is distinguished from it by the tendency of the last whorl of the shell to become separated from the parietal wall in adults,

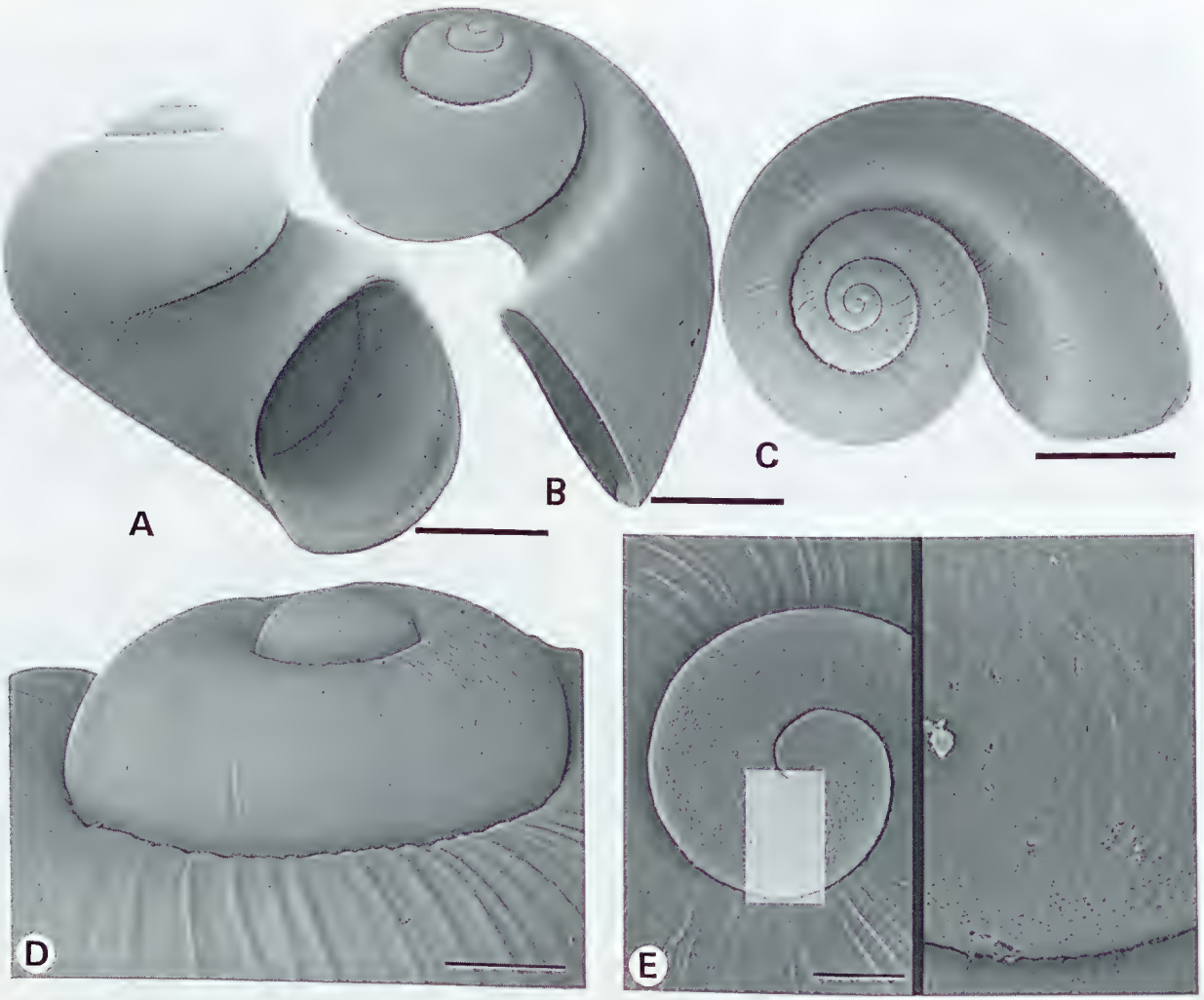


**Fig.13.** *Jardinella corrugata* n.sp., shell. A–C, shell, Stn 73(C); D–E, protoconch, Stn 73(C), D, side view; E, dorsal view and microsculpture. The highlighted area shows the area magnified in the adjacent frame a further 4X. Scales:- A,B,C – 1.0 mm, D,E – 0.1 mm.

by the presence of sharp axial riblets, and a wider umbilicus [mean width relative to shell width 0.2 (males) and 0.3 (females) compared with 1.5 (males) and 1.1 (females) in *J. edgbastonensis*]. Of the shell and opercular characters measured, shell length and width, number of teleoconch whorls, aperture length and width, body whorl length, convexity, spire angle, umbilical width, opercular length, and the length of the white smear on the operculum are all significantly different (P equal to or less than 0.001), as are protoconch diameter and number of protoconch whorls (P equal to or less than 0.005). The two species also separate very well in the discriminate analysis (Figs 35-37), and *J. corrugata* also discriminates markedly from all other taxa.

Several anatomical characters separate *J. edgbastonensis* and *J. corrugata*, particularly genital differences. The pigmented penis is expanded and flattened (lobed) distally whereas that of *J. edgbastonensis* is unpigmented and narrow distally (compare Figs 10C and A, and 11D and A,B). The female genitalia differ mainly in the relative proportions of the oviduct glands and the development of the vestibule, the glandular oviduct being relatively short and broad compared with that of *J. edgbastonensis* (compare Figs 12C and A). The vestibule is much more massive in *J. corrugata*, with the oviducal opening placed higher and the bursa copulatrix is relatively larger and longer. In addition the oviduct anterior to the opening of the seminal receptacle is straight in *J. corrugata* but has a fold in *J. edgbastonensis* (compare Fig. 12D and B).

Although this species has only been collected from two springs at Edgbaston Springs, it may possibly occur in some of the other springs in the Edgbaston Group.

**Etymology.** From the Latin word *corrugo*, meaning to wrinkle up.

### *Jardinella coreena* n.sp.

**Type locality.** Z14, large unnamed spring just south of "Coreena" homestead, about 32 km north-east of Barcaldine, 23°17'S 144°24'E. Longreach 337 425. WZ, 5 May 1988.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn Z14 C.156792 (holotype), C.156793 (12 paratypes), SAM D.18529 (100+ paratypes), QM MO.20077 (2 paratypes).

**Diagnosis.** Shell trochiform, of medium size (up to 3.1 mm in length), smooth, umbilicate. Penis with distal lobe, unpigmented. Pallial oviduct with wide vestibule, pallial opening ventral and anterior to capsule gland.

**Description.** *Shell* (Figs 6F, 14E,F): trochiform, of medium size, 2.61-3.09 mm in length [mean 2.72 (M), 2.84 (F)]; 2.17-2.55 mm in width [mean 2.27 (M), 2.36 (F)]; not sexually dimorphic in size (P greater than 0.2); of medium thickness, translucent to opaque white, with indistinct, transparent periostracum. Spire angle 76.58-89.9° [mean 79.07 (M), 80.86 (F)]. Protoconch (Fig. 14F) of 1.25-1.3 whorls [mean 1.25 (M), 1.26 (F)]. Teleoconch of 2.55-3.1 convex whorls [mean 2.85 (M), 2.93 (F)]. Convexity ratio 0.24-0.31 [mean 0.28 (M), 0.27 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.52-0.56 [mean 0.55 (M), 0.54 (F)]. Inner lip of medium thickness, of medium width. Outer lip prosocline, angle 15.97-28.84° [mean 23.93 (M), 21.12 (F)]. Umbilicus of medium width [0.22-0.4 mm in width; mean 0.27 (M), 0.34 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 2.97 mm, width 2.47 mm, length of aperture 1.59 mm, number of teleoconch whorls 2.80.

*Operculum* (Fig. 15A): thin, yellow, 1.22-1.4 mm in length [mean 1.26 (M), 1.31 (F)]. Without white smear. Ratio of opercular length to position of nucleus 3-3.58 [mean 3.41 (M), 3.19 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 15B,C): each central tooth with 3-4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.6-1.7; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula 2.1.(3-4); ratio of length of primary cusp/length of adjacent outer cusps 1.5-1.7; with well-developed basal bulge; outer shaft 1.8-1.9 times longer than cutting edge.

*Head-foot:* cephalic tentacles triangular in section; lacking obvious dorsal and ventral ciliated tracts. Head and foot grey to dark grey; distal end of cephalic tentacles sometimes unpigmented. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 25-28 filaments; apex on right. Osphradium between posterior end and middle of ctenidium to near middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum without arch, position of anus varies from near mantle edge to intermediate position. Kidney either behind, or extends forward slightly into, pallial roof.

*Male reproductive system* (Figs 10B, 11C): penial lobe in medial part of distal part of penis; distal end of penis tapering; penis unpigmented. Vas deferens with one loop/coil anterior to prostate gland.

*Female reproductive system* (Fig. 12E,F): pallial oviduct with ventral channel modified as wide, muscular vestibule, duct extended anterior to capsule gland as ventrally located papilla. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix, which lies posteroventral to, and smaller to subequal in size to, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct basically U-shaped but with extra bend distally. Rudimentary penis absent in females.

**Remarks.** This species is isolated from the others in the

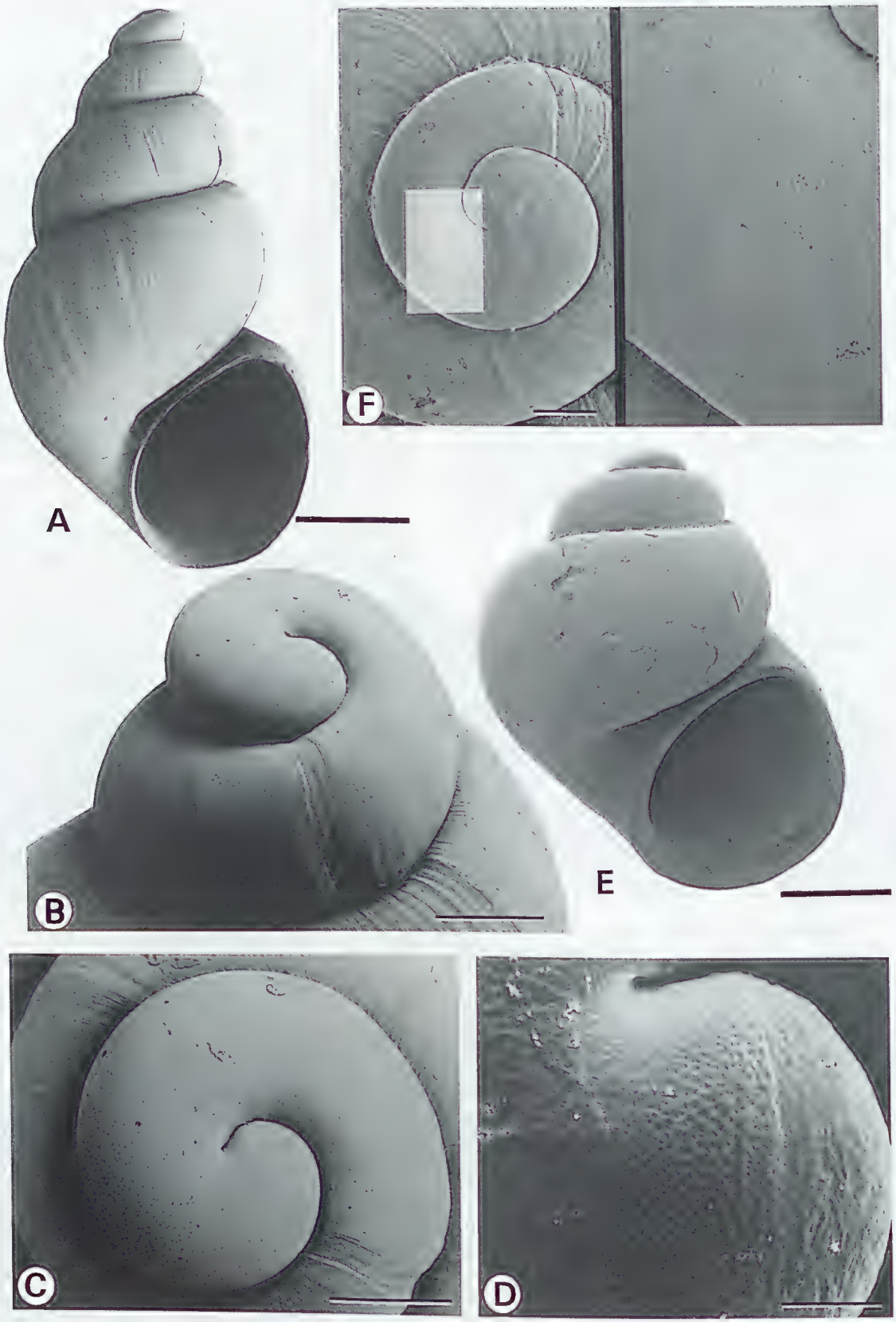


**Fig.14.** Shells of *Jardinella jesswiseae* n.sp. and *J. coreena* n.sp. A–D, *J. jesswiseae*, Stn 73(A); A, shell; B–D, protoconch, D showing microsculpture. E, F, *J. coreena*, Stn Z14; E, shell; F, protoconch, dorsal view and microsculpture. The highlighted area shows the area magnified in the adjacent frame a further 4X. Scales:- A,E – 0.5 mm, B,C,F – 0.1 mm, D – 0.02 mm.

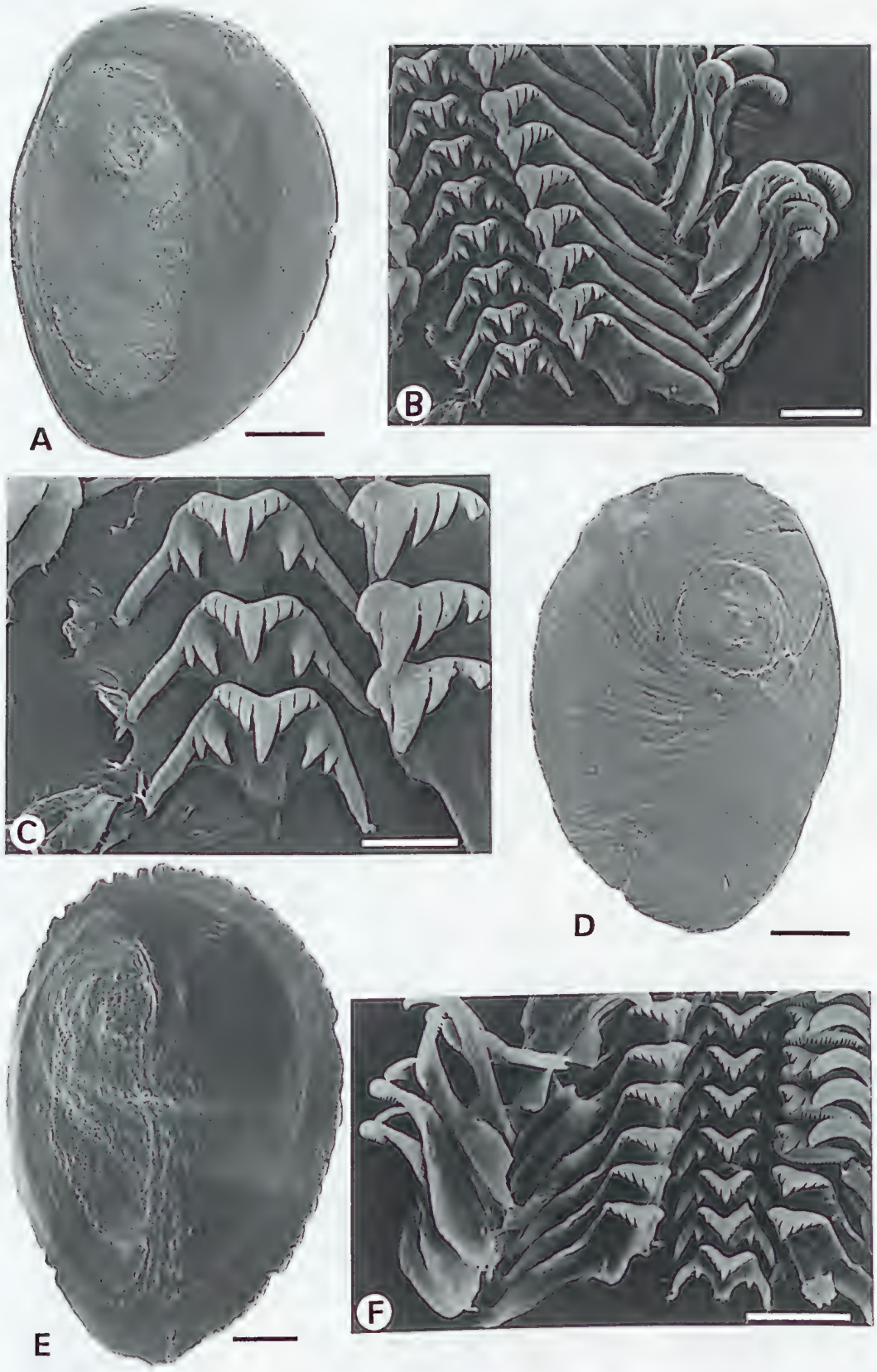


**Fig.15.** *Jardinella coreena* n.sp. and *Jardinella jesswiseae* n.sp., opercula and radulae. A–C, *J. coreena*, Stn Z14; A, inner view of operculum; B,C, radula, C showing detail of central and lateral teeth. D–F, *J. jesswiseae*, Stn 73(A); D,E, outer (D) and inner (E) sides of operculum; F, radula. Scales:- A,D,E – 0.1 mm, B,F – 0.02 mm, C – 0.01 mm.

area, being found 61 km south of the main Edgbaston Spring Group. It most closely resembles *J. edgbastonensis* n.sp. in shell characters but has a slightly smaller shell (P less than 0.3 for shell length and P less than 0.003 for shell width). Other shell characters that differ (P less than 0.006) include the number of protoconch whorls and the protoconch diameter (*J. edgbastonensis* is larger). Another similar species, *J. carnarvonensis* n.sp., is contrasted below. In the discriminate analysis the "trochiform" species do not separate well (with the exception of *J. corrugata* n.sp.). Comparisons of their generalised distances (Table 5) shows that *J. coreena* and *J. edgbastonensis* are the two most similar species, *J. carnarvonensis* the next most similar. The Euclidean distance comparisons (Table 6) show that *J. edgbastonensis* is the most similar but the next most similar species are *J. eulo* n.sp. and *J. isolata* n.sp., both these species being contrasted below.

Anatomically *J. coreena* also resembles *J. edgbastonensis*, having somewhat similar female genital characters, although differing in detail, notably in a more expanded vestibule and in having a small fold in the oviduct on both sides of the duct of the seminal receptacle. The penis has an expanded distal end (i.e. is lobed) and, apart from being unpigmented, is more similar to that of *J. corrugata*, not *J. edgbastonensis*. It would, however, be possible to derive the penis of *J. edgbastonensis* from that of *J. coreena* (or *J. corrugata*) by reduction of the folds. It also shares a general resemblance in shell characters to the two species described from the second group of springs (*J. carnarvonensis* and *J. exigua* n.sp.) but differs from them in its larger size and in genital characters.

**Etymology.** The species is named after the Coreena Homestead.

### *Jardinella pallida* n.sp.

**Localities.** Stn 72, unnamed spring 2.3 km north-east of "Edgbaston" homestead, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaburra 338 486. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 220 m, on open plain. A – general; B – head of spring, in *Phragmites*; D – middle of outflow 50 m from head; E – edge of outflow 50 m from head; F – 20 m from end of outflow. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep. Stn 74, unnamed spring about 3.6 km south-east of "Edgbaston" homestead, about 30 km north-east of Aramac, 22°45'30"S 145°25'30"E. Muttaburra 339 483. WFP and PHC, 26 Sept. 1984. Small spring in low sandhills on the edge of a claypan. Stn Z7, unnamed spring about 2.4 km north-east of "Edgbaston" homestead, about 33 km east of Aramac, 22°42'45"S 145°25'25"E. Muttaburra 338 487. WZ, 3 May 1988. No mound but extensive seepage. Stn Z8, unnamed spring about 2.3 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°43'S 145°25'30"E. Muttaburra 338 487. WZ, 3 May 1988. Low mound with outflow of about 60 m. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WZ, 4 May 1988. Large spring. A – outflow (= Stn 73). Stn Z10, unnamed spring about 3.3 km south-east of "Edgbaston" homestead, about 31 km east of Aramac, 22°45'30"S 145°25'40"E. Muttaburra 339 483. WZ, 4 May 1988.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 73(A) C.156759 (holotype), C.156760 (270 paratypes), Stn 73(B) C.156762 (10 paratypes), Stn 73(C) C.156761 (5 paratypes), Stn 72(A) C.156763 (80 paratypes), Stn 72(B) C.156767 (10 paratypes), Stn 72(D) C.156764 (90 paratypes), Stn 72(E) C.156766 (45 paratypes), Stn 72(F) C.156765 (340 paratypes), Stn 74 C.156768 (100+ paratypes), Stn Z7 C.157425 (1 paratype), Stn Z8 C.157426 (2 paratypes), Stn Z10 C.157423 (2 paratypes), SAM Stn Z7 D.18530 (30+ paratypes), Stn Z8 D.18531 (15 paratypes), Stn Z9(A) D.18532 (6 paratypes), Stn Z10 D.18533 (20+ paratypes), QM Stn 73(A) MO.20078 (5 paratypes).

**Diagnosis.** Shell conical, small (up to 1.8 mm in length), smooth, narrowly umbilicate. Penis lacking distinct lobe(s) but with median, pigmented part of distal portion swollen and with long, narrow papilla. Pallial oviduct with narrow vestibule, pallial opening subterminal and subventral.

**Description.** *Shell* (Figs 16B, 17C,D,G,H): conic, small, 1.34-1.82 mm in length [mean 1.41 (M), 1.62 (F)]; 0.82-1.03 mm in width [mean 0.86 (M), 0.94 (F)]; sexually dimorphic in size (P less than 0.001); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 58.97-77.4° [mean 73.52 (M), 68.88 (F)]. Protoconch (Fig. 17C,G,H) of 1.2-1.3 whorls [mean 1.24 (M), 1.24 (F)]. Teleoconch of 2.15-2.6 convex whorls [mean 2.25 (M), 2.45 (F)]. Convexity ratio 0.12-0.29 [mean 0.19 (M), 0.22 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.39-0.47 [mean 0.43 (M), 0.42 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 11.32-27.96° [mean 21.06 (M), 16.71 (F)]. Umbilicus small [0-0.12 mm in width; mean 0.06 (M), 0.05 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 1.77 mm, width 0.96 mm, length of aperture 0.67, number of teleoconch whorls 2.50.

*Operculum* (Fig. 18C): thin, very pale yellow, 0.59-0.77 mm in length [mean 0.63 (M), 0.70 (F)]. With or without white smear up to 0.3 mm in length [mean 0.13 (M), 0.15 (F)]. Ratio of opercular length to position of nucleus 2.68-4.28 [mean 3.36 (M), 3.30 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 18D): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.4-1.6; 2 pairs of basal denticles; dorsal edge concave; basal process long, tongue shaped. Each lateral tooth with cusp formula (3-4).1.5; ratio of length of primary cusp/length of adjacent outer cusps 1.5-1.6; with well-developed basal bulge; outer shaft 1.9 times longer than cutting edge.

*Head-foot:* cephalic tentacles triangular in section, with dorsal ciliated band present on both tentacles; 3 ciliated bands along most of ventral surface. Unpigmented except for smudge of grey behind eyes and proximal sides of snout. Visceral coil essentially unpigmented.

**Anatomy.** *Mantle cavity:* ctenidium with 20-22 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus near mantle edge. Kidney extending well forward into pallial roof.

*Male reproductive system* (Figs 20H, 21A): distinct penial lobe(s) absent but these represented by swollen median part of distal portion of penis; distal end of penis with long papilla; penis unpigmented except pale grey distal end (excluding papilla). Vas deferens with about 2 loops/coils anterior to prostate gland.

*Female reproductive system* (Fig.20F,G): pallial oviduct with ventral channel modified as narrow, muscular vestibule located subventrally, opening subterminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is smaller than, albumen gland. Coiled oviduct and bursal duct fused to form common duct about halfway to posterior pallial wall

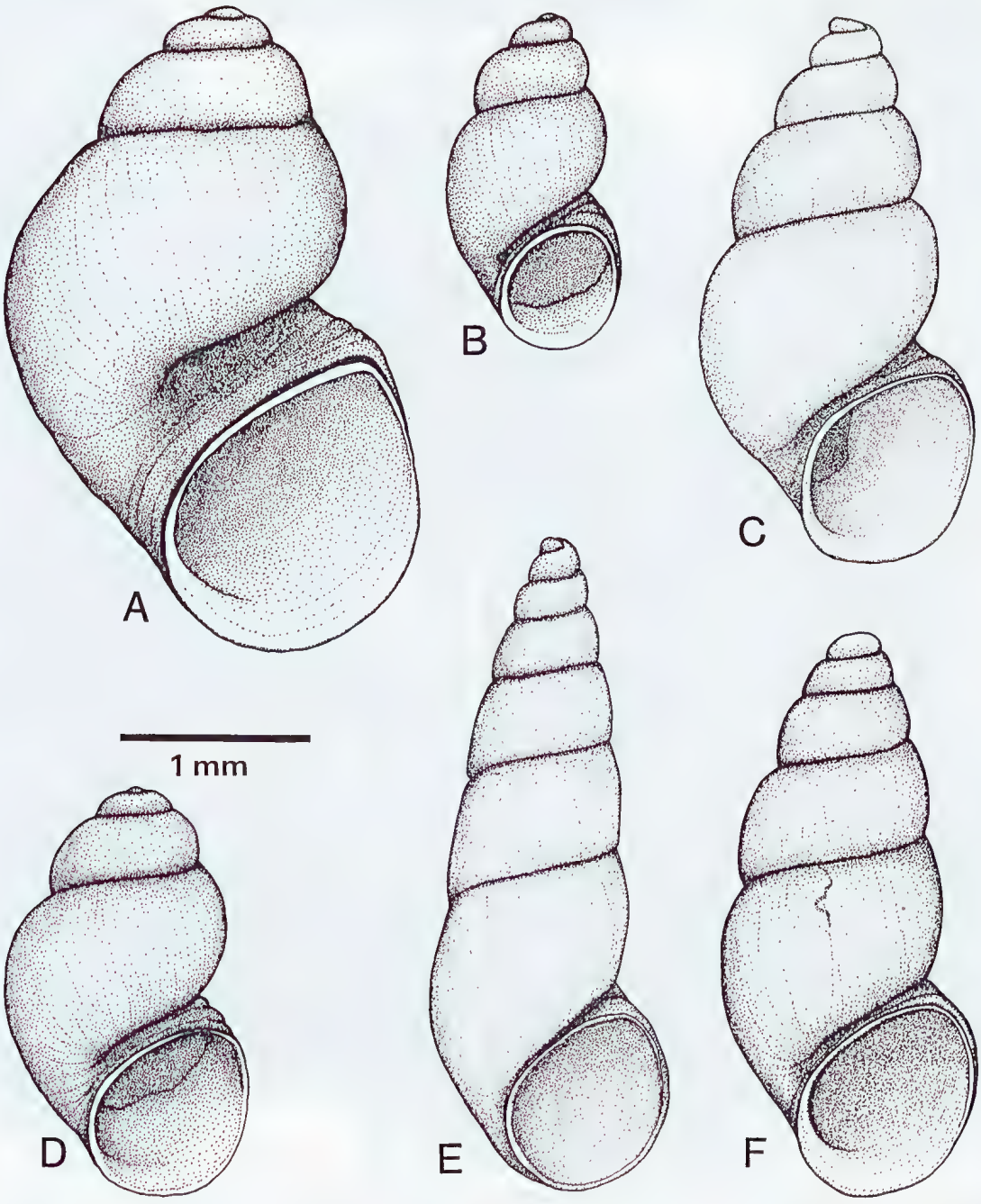


**Fig.16.** Shells of holotypes of species of *Jardinella*. A, *J. isolata*; B, *J. pallida*; C, *J. jesswiseae*; D, *J. colmani*; E, *J. acuminata*; F, *J. zeidlerorum*.

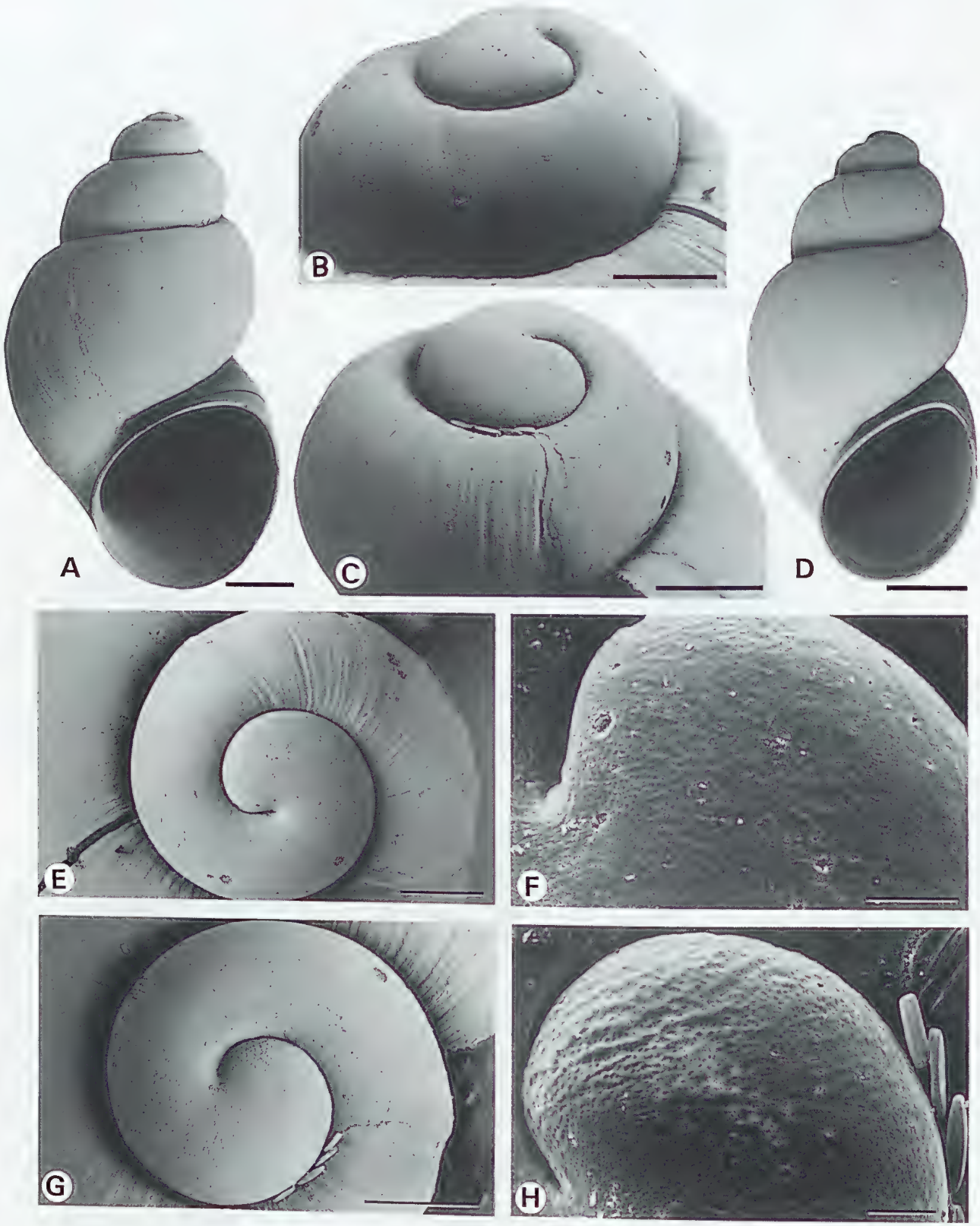


**Fig.17.** Shells of *Jardinella colmani* n.sp. and *J. pallida* n.sp. A,B,E,F, *J. colmani*, Stn 71; A, shell; B, E,F, lateral (B) and dorsal (E,F) views of protoconch, F showing microsculpture. C,D,G,H, *Jardinella pallida*, Stn 73(A); C, lateral view of protoconch, D, shell, G, H, dorsal view of protoconch and microsculpture (H). Scales:- A,D – 0.3 mm, B,C,E,G – 0.1 mm, F,H – 0.02 mm.

from seminal receptacle duct. Coiled oviduct basically U-shaped but with extra bend distally. Rudimentary penis absent in females.

**Remarks.** This species and the next appear to be closely related and are contrasted below. This species is the smallest in the Edgbaston Springs, being readily distinguished from all of the other species by its small size, pale body colour and medium-conical spire shape. It lives in the outflows of the springs in sympatry with all of the other species (see Table 4), being most abundant in Stn 72 in the lower outflow and in the upper outflow of Stn 73, but occurring throughout both springs.

**Etymology.** From the Latin word *pallidus* (a) meaning pale.

### *Jardinella colmani* n.sp.

**Localities.** Stn 71, unnamed spring near Smokey Creek about 8 km east-north-east of "The Springs" homestead, about 83 km north-north-east of Aramac, 22°12'20"S 145°22'30"E. Muttaburra 332 544. WFP and PHC, 25 Sept. 1984. Stn Z6, unnamed spring about "11 km north-east of "The Springs" homestead, about 83 km north of Aramac", 22°12'20"S 145°22'30"E. Muttaburra 332 544. WZ, 2 May 1988. Low mound (fenced) with ill-defined source and small outflow (almost certainly the same spring as Stn 71).

**Material examined.** HOLOTYPE AND PARATYPES – (all Stn 71) AMS C.156776 (holotype), C.156777 (500+ paratypes), SAM Stn Z6 D.18534 (2 paratypes), D.18535 (20 paratypes), QM MO.20079 (5 paratypes).

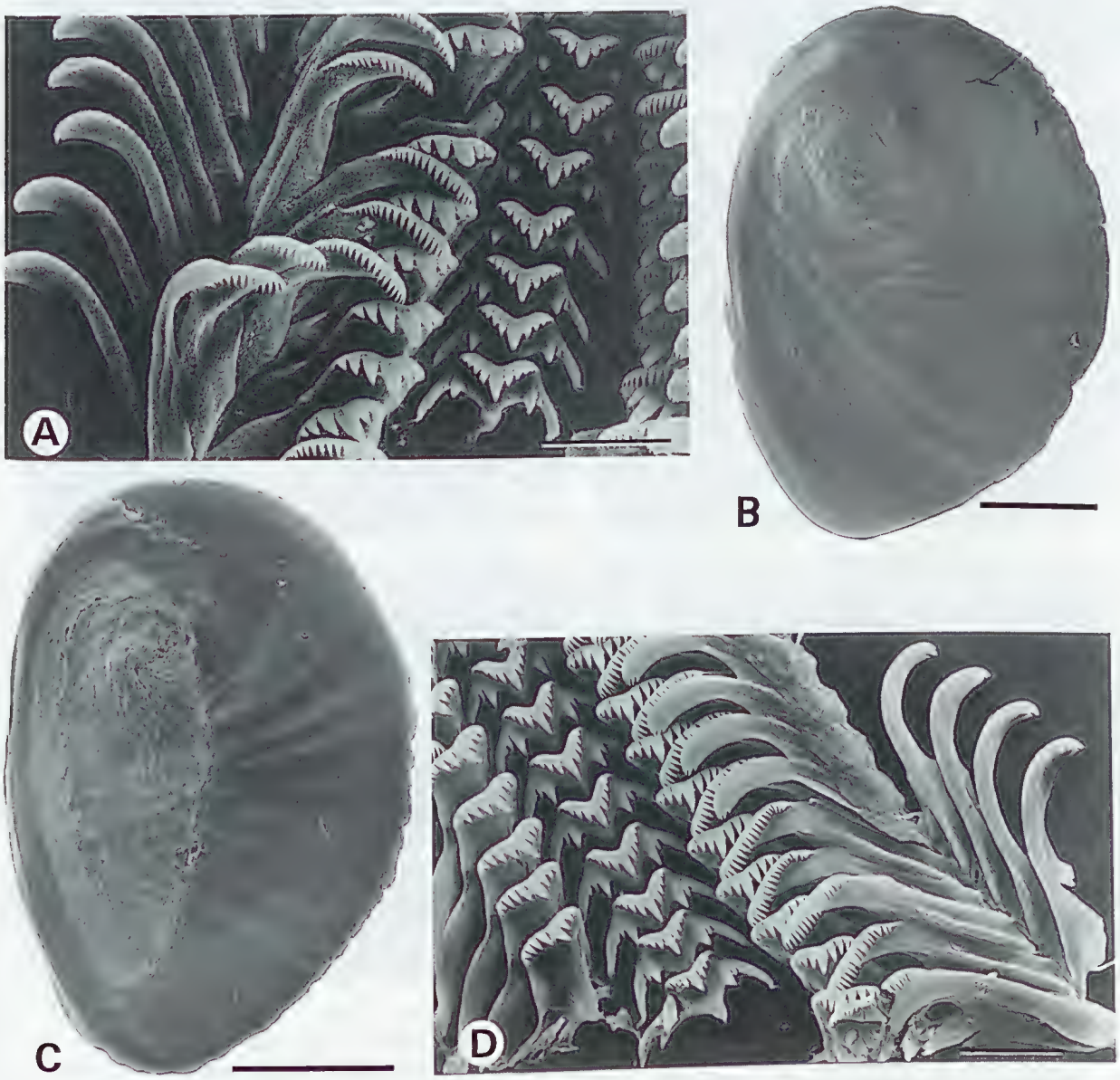


**Fig.18.** *Jardinella colmani* n.sp. and *Jardinella pallida* n.sp., opercula and radulae. A,B, *J. colmani*, Stn 71; A, radula; B, inner side of operculum. C,D, *J. pallida*, Stn 73(A); C, inner side of operculum; D, radula. Scales:- A,D – 0.01 mm, B,C – 0.2 mm.

**Diagnosis.** Shell conical, small to medium (up to 2.3 mm in length), smooth, narrowly umbilicate. Penis with slightly swollen area medially behind tapering distal end; swollen part (medial) pigmented. Pallial oviduct with narrow vestibule, pallial opening located on prominent lateral, subterminal papilla.

**Description.** *Shell* (Figs 16D, 17A,B,E,F): conic, small to medium size, 1.6-2.31 mm in length [mean 1.66 (M), 1.96 (F)]; 1.02-1.48 mm in width [mean 1.11 (M), 1.26 (F)]; sexually

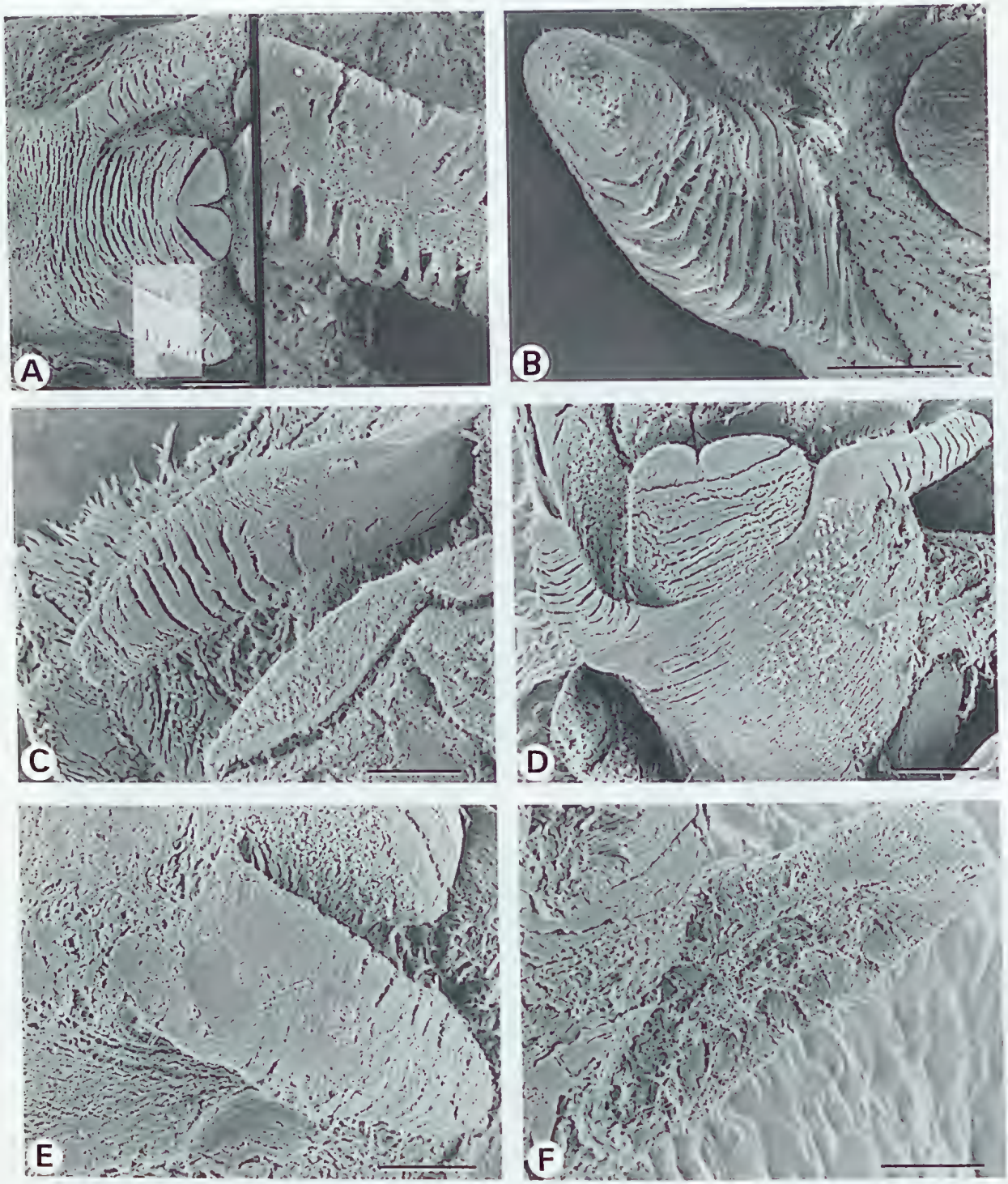


**Fig.19.** Scanning electron micrographs of critically point dried cephalic tentacles of species of *Jardinella*. A,B, *J. colmani*, Stn 71; A, dorsal view of head, the highlighted area showing detail of cilia on right tentacle at 4X additional magnification; B, ventral view of left tentacle with part of the snout also showing. C,D, *J. zeidlerorum*, Stn Z12; C, ventral view of left tentacle with part of anterior edge of foot also showing; D, dorsal view of head showing cilial tract at base of right tentacle. E,F, *J. jesswiseae*, Stn 73(A); E, dorsal view of right tentacle; F, ventral view of left tentacle. Scales:- A,D – 0.1 mm, B,C,E,F – 0.05 mm.

dimorphic in size (P less than 0.002); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 70.95-86.79° [mean 82.83 (M), 77.19 (F)]. Protoconch (Fig. 17B,E,F) of 1.2-1.35 whorls [mean 1.26 (M), 1.27 (F)]. Teleoconch of 2-2.65 convex whorls [mean 2.20 (M), 2.45 (F)]. Convexity ratio 0.16-0.28 [mean 0.22 (M), 0.21 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.42-0.51 [mean 0.47 (M), 0.44 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 5.39-28.31° [mean 12.57 (M), 15.74 (F)]. Umbilicus small [0.05-0.13 mm in width; mean 0.09 (M), 0.09 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 2.11 mm, width 1.30 mm, length of aperture 0.88, number of teleoconch whorls 2.50.

*Operculum* (Fig. 18B): thin, very pale yellow, 0.69-0.95 mm in length [mean 0.75 (M), 0.85 (F)]. With or without white smear up to 0.37 mm in length [mean 0.00 (M), 0.04 (F)], without pegs (note: of a sample of 21 only females had any sort of white smear). Ratio of opercular length to position of nucleus 2.63-3.52 [mean 3.05 (M), 3.04 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 18A): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.6-1.7; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp

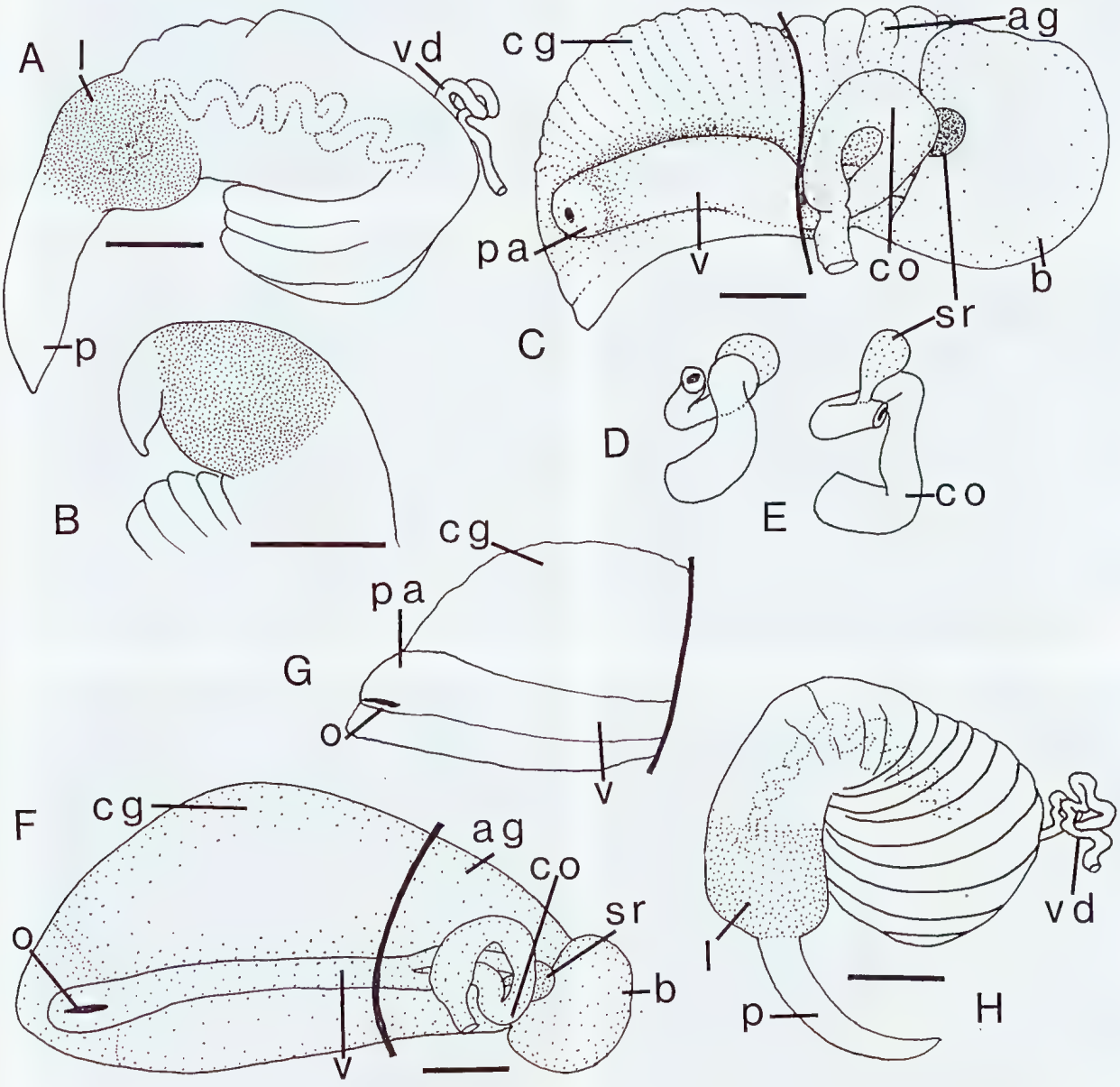


**Fig.20.** Genitalia of species of *Jardinella*. A–E, *J. colmani*, Stn 71, A,B, penis, showing the range of variation in the length of the penial papilla; C–E, oviduct; F–H, *J. pallida*, Stn 73(A), F,G, oviduct, H, penis. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; pa – papilla with oviduct opening; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:- A,C,F,H – 0.1 mm, B – 0.2 mm.

formula 3.1.3-4; ratio of length of primary cusp/length of adjacent outer cusps 1.3-1.6; with well-developed basal bulge; outer shaft 1.3-1.4 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Fig.19A,B) triangular in section, with 1 mid-dorsal ciliated band on right tentacle only and 3 ventral bands on both tentacles. Proximal sides of snout and bases of cephalic tentacles black or grey, pigment extending along sides of neck. Cephalic tentacles with mid-dorsal streak in proximal half in some specimens; sides of foot and opercular lobe pale grey.

**Anatomy.** *Mantle cavity:* ctenidium with 17-23 filaments; apex on right. Osphradium between posterior end and

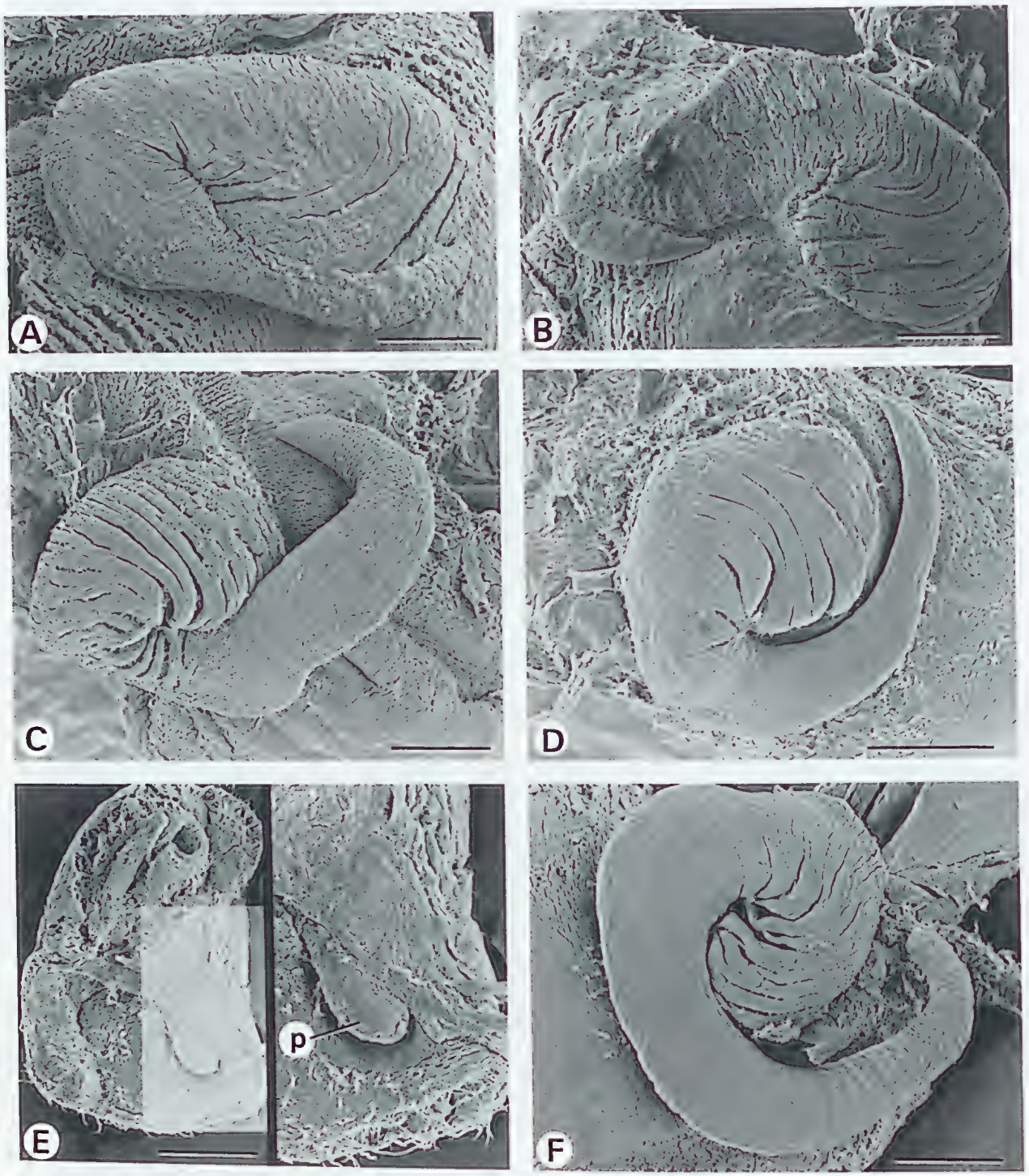


**Fig.21.** Scanning electron micrographs of critical point dried genitalia of species of *Jardinella*. A, *J. pallida*, Stn 73(A), penis; B, E, *J. colmani*, Stn 71, B, penis; E, glandular oviduct, the highlighted area is magnified 2X in the adjacent figure and shows the papilla-like structure with the pallial opening at its anterior end; C, *J. jesswiseae*, Stn 73(A), penis; D, *J. acuminata*, Stn 73(B), penis; F, *J. zeidlerorum*, Stn Z12, penis. p – papilla. Scales:- A – 0.05 mm, B,C,D,F – 0.1 mm, E – 0.2 mm.

middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus with intermediate position relative to mantle edge. Kidney extending well forward into pallial roof.

*Male reproductive system* (Figs 20A,B, 21B): penial lobe not obvious, appears to be developed as medial (pigmented) swollen area; distal portion tapering, distal extremity with very short papilla in some specimens; swollen medial area grey, rest unpigmented. Vas deferens with few loops/coils anterior to prostate gland.

*Female reproductive system* (Figs 20C–E, 21E): pallial oviduct with ventral channel modified as narrow, lateroventrally placed muscular vestibule, duct extended as prominent lateral papilla opening laterally and subterminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from anterodorsal side of ovate bursa copulatrix which lies posterior to, and is slightly larger than, albumen gland. Coiled oviduct and bursal duct fused to form common duct about halfway to posterior pallial wall from seminal receptacle duct. Coiled oviduct basically U-shaped but with extra bend in middle part. Rudimentary penis absent in females.

**Remarks.** This species is most similar to *J. pallida* n.sp. and the two taxa are located about 58 km apart. *Jardinella colmani* differs from *J. pallida* in its larger size darker body pigmentation and more developed vestibule, the opening of which is located on a distinct papilla midlaterally on the anterior part of the capsule gland. The penis is similar in both species but the long, distal filament is narrower, relative to the rest of the penis, in *J. pallida* than in *J. colmani*.

Discriminate analysis shows *J. colmani* to be most similar to *J. pallida* and both species are more similar to one another than to any other species. Comparisons of the measurement data showed that all shell and opercular characters, except convexity, the number of teleoconch and protoconch whorls and aperture angle, differ significantly (P less than 0.001) from those of *J. pallida*. The only other somewhat similar species is *J. jesswiseae* n.sp. which is more darkly pigmented, has a taller shell with more whorls and a deviated protoconch, as well as several anatomical differences.

A visit to what is almost certainly the same spring in 1987 by W. Zeidler failed to locate living material of *J. colmani* (2 empty shells were found) so the population may have considerably declined in numbers or even be extinct.

**Etymology.** The species is named after Phillip Colman of the Australian Museum.

### *Jardinella jesswiseae* n.sp.

**Localities.** Stn 72, unnamed spring 2.3 km north-east of "Edgbaston" homestead, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaburra 338 486. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 220 m, on open plain. A – general; B – head of spring, in *Phragmites*; D – middle of outflow 50 m from head; E – edge of outflow 50 m from head; F – 20 m from end of outflow. Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep; D – head of spring. Stn 74, unnamed spring about 3.6 km south-east of "Edgbaston" homestead, about 30 km north-east of Aramac, 22°45'30"S 145°25'30"E. Muttaburra 339 483. WFP and PHC, 26 Sept. 1984. Small spring in low sandhills on the edge of a claypan. Stn Z7, unnamed spring about 2.4 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°42'45"S 145°25'25"E. Muttaburra 338 487. WZ, 3 May 1988. No mound but extensive seepage. Z8, unnamed spring about 2.3 km north-east of "Edgbaston" homestead, about 33 km north-east of Aramac, 22°43'S 145°25'30"E. Muttaburra 338 487. WZ, 3 May 1988. Low mound with outflow of about 60 m. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain (= Stn 73). Stn Z10, unnamed spring about 3.3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'30"S 145°25'40"E. Muttaburra 339 483. WZ, 4 May 1988.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 73(B) C.156748 (holotype), C.156749 (330 paratypes), Stn 73(C) C.156750 (45 paratypes), Stn 73(A) C.156751 (1620 paratypes), Stn 73(D) C.156752 (165 paratypes), Stn 72(A) C.156753 (300+ paratypes), Stn 72(B) C.156757 (9 paratypes), Stn 72(D) C.156754 (460 paratypes), Stn 72(E) C.156756 (20 paratypes), Stn 72(F) C.156755 (40 paratypes), Stn 74 C.156758 (500+ paratypes), Stn Z10 C.157422 (4 paratypes), Stn Z7 C.157424 (2 paratypes), Stn Z8 C.157427 (2 paratypes), SAM Stn Z7 D.18536 (50+ paratypes), Stn Z8 D.18537 (500+ paratypes), Stn Z9(A) D.18538 (500+ paratypes), Stn Z9(B) D.18539 (1 paratype), Stn Z10 D.18540 (30+ paratypes), QM Stn 73(B) MO.20080 (5 paratypes).

**Diagnosis.** Shell conical, small to medium in size (up to 2.8 mm in length), smooth, umbilicate. Penis with expanded, pigmented distal half, lacking distinct lobe(s), with small terminal papilla. Pallial oviduct with wide vestibule, pallial opening ventral and subterminal.

**Description.** *Shell* (Figs 14A–D, 16C): conical, small to medium size, 1.87-2.84 mm in length [mean 2.08 (M), 2.43 (F)]; 1.09-1.4 mm in width [mean 1.18 (M), 1.29 (F)]; sexually dimorphic in size (P less than 0.003); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 46.83-63.09° [mean 57.06 (M), 55.35 (F)]. Protoconch (Fig. 14B–D) deviated; of 1.2-1.4 whorls [mean 1.26 (M), 1.25 (F)]; minutely pitted. Teleoconch of 2.9-3.85 convex whorls [mean 3.20 (M), 3.55 (F)]. Convexity ratio 0.13-0.24 [mean 0.20 (M), 0.20 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.33-0.45 [mean 0.40 (M), 0.37 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 10.25-28.15° [mean 19.73 (M), 20.16 (F)]. Umbilicus minute to

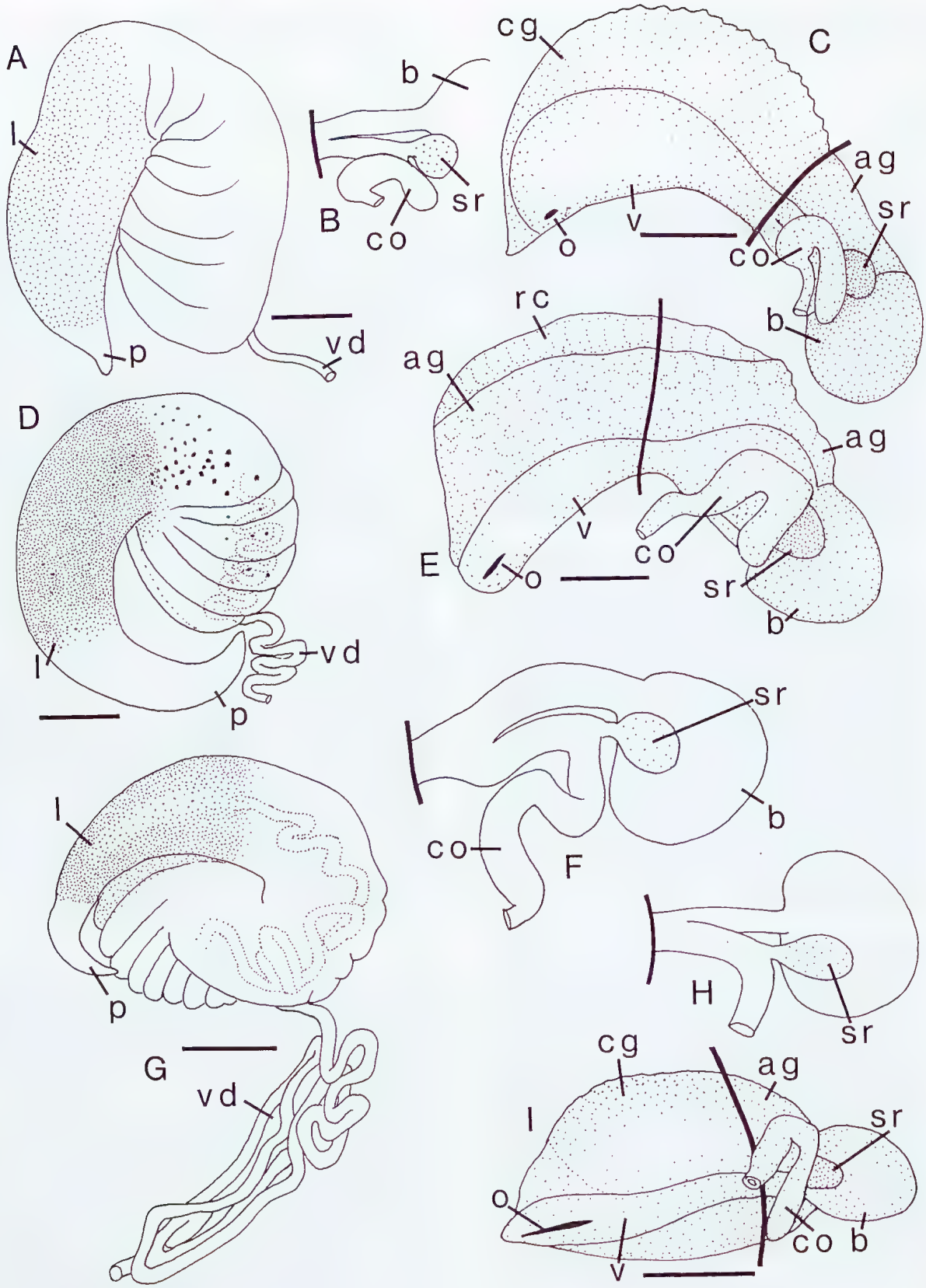


**Fig.22.** Genitalia of species of *Jardinella*. A–C, *J. jesswiseae*, Stn 73(A), A, penis, B,C, oviduct; D–F, *J. zeidlerorum*, Stn Z12, D, penis, E,F, oviduct; G–I, *J. acuminata*, Stn 73(B), G, penis, H,I, oviduct. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:- A,D,G – 0.1 mm, C,E,I – 0.2 mm.

closed [0-0.07 mm in width; mean 0.03 (M), 0.04 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 2.86 mm, width 1.42 mm, length of aperture 0.98 mm, number of teleoconch whorls 3.75.

*Operculum* (Fig. 15D,E): thin, very pale yellow, 0.71-0.95 mm in length [mean 0.80 (M), 0.88 (F)]. Without white smear. Ratio of opercular length to position of nucleus 3.21-4.25 [mean 3.80 (M), 3.70 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 15F): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.7-1.9; 1 pair of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula 3.1.4; ratio of length of primary cusp/length of adjacent outer cusps 1.3-1.5; with well-developed basal bulge; outer shaft 2-2.1 times longer than cutting edge. Inner and outer marginal teeth with cusps about equal in size.

*Head-foot:* cephalic tentacles (Fig. 19E,F) triangular in section, with dorsal ciliated band present on right tentacle only; distinct ciliated band along most of ventral surface. Head and foot black with black cephalic tentacles except for narrow unpigmented mid-dorsal line. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 24-32 filaments; apex on right, or towards centre. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus distant from mantle edge. Kidney extends forward slightly into pallial roof.

*Male reproductive system* (Figs 21C, 22A): distinct penial lobe(s) absent but distal, pigmented part of penis swollen; distal extremity of penis with short papilla; distal half of penis (except papilla) grey, distal part of base grey or unpigmented, rest of base unpigmented. Vas deferens with few loops/coils next to anterior extremity of prostate gland.

*Female reproductive system* (Fig. 22B,C): pallial oviduct with ventral channel modified as wide muscular vestibule, opening subterminal and ventral and thickened to form very short papilla- like structure. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is slightly smaller than, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis present in some females.

**Remarks.** *Jardinella jesswiseae* is the most abundant of the Edgbaston snails in the middle part of the outflows (Table 4). In shell characters it is most similar to *J. zeidlerorum* n.sp., as also shown by discriminate analysis (Tables 5,6; Figs 35–37). It is distinguished from that species by its smaller size, uniformly black body (visible through the shell), rather tall spire, more convex whorls and deviated protoconch. The genitalia are similar except that the vestibule is more expanded in *J. jesswiseae*.

The two following species are similar to *J. jesswiseae* but have even more elongate shells.

**Etymology.** The species is named for Mrs Jess Wise, a long serving volunteer in the malacology section of the Australian Museum.

### *Jardinella zeidlerorum* n.sp.

**Locality.** Stn Z12, unnamed spring about 11 km south-south-east of "Edgbaston" homestead, about 0.8 km south of main road, about 28 km north-east of Aramac, 22°47'20"S 145°25'40"E. Muttaburra 339 479. WZ, 4 May 1988. Mud mound supporting large natural pool.

**Material examined.** HOLOTYPE AND PARATYPES – (all Stn Z12) AMS C.156790 (holotype), C.156791 (18 paratypes), SAM D.18541 (200+ paratypes), QM MO.20081 (2 paratypes).

**Diagnosis.** Shell elongate conic, of medium size (up to 2.9 mm in length), smooth, non-umbilicate. Penis lacking lobe(s), pigmented medially, distal end tapering. Pallial oviduct with unmodified ventral channel, pallial opening terminal and ventral.

**Description.** *Shell* (Figs 16F, 23D–F): elongate conic, of medium size, 2.41-2.93 mm in length [mean 2.57 (M), 2.62 (F)]; 1.16-1.46 mm in width [mean 1.19 (M), 1.25 (F)]; not sexually dimorphic in size (P greater than 0.1); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 42.72-47.65° [mean 44.39 (M), 45.28 (F)]. Protoconch (Fig. 23E,F) strongly deviated; of 1.25-1.3 whorls [mean 1.25 (M), 1.26 (F)]. Teleoconch of 3.75-4.4 convex whorls [mean 4.15 (M), 4.05 (F)]. Convexity ratio 0.1-0.17 [mean 0.12 (M), 0.14 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.35-0.4 [mean 0.36 (M), 0.38 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 1.05-7.67° [mean 4.18 (M), 3.95 (F)]. Umbilicus closed.

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 2.92 mm, width 1.30 mm, length of aperture 0.96 mm, number of teleoconch whorls 4.25.

*Operculum* (Fig. 24B): thin, very pale yellow, 0.71-0.9 mm in length [mean 0.76 (M), 0.79 (F)]. With white smear 0.22-0.43 mm in length [mean 0.26 (M), 0.30 (F)]. Ratio of opercular length to position of nucleus 3.46-4.61 [mean 4.13 (M), 4.04 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 24D,E): each central tooth with 4-5 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.2-1.4; 2 pairs of basal denticles; dorsal edge inverted U-shaped; basal process long, tongue shaped. Each lateral tooth with cusp formula (3-4).1.5; ratio of length of primary cusp/length of adjacent outer cusps 1.3-1.4; with well-developed basal bulge; outer shaft 1.7-1.9 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Fig. 19C,D) triangular in section, with dorsal ciliated band present on right tentacle only; scattered ventral cilia only (this latter observation not entirely certain as the preparations are not very good). Head and foot black, distal end of tentacles unpigmented but with black pigment dorsally in proximal part and narrow stripe in distal part; eye surrounded by heavy narrow unpigmented ring. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 24-27 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. Thinly developed

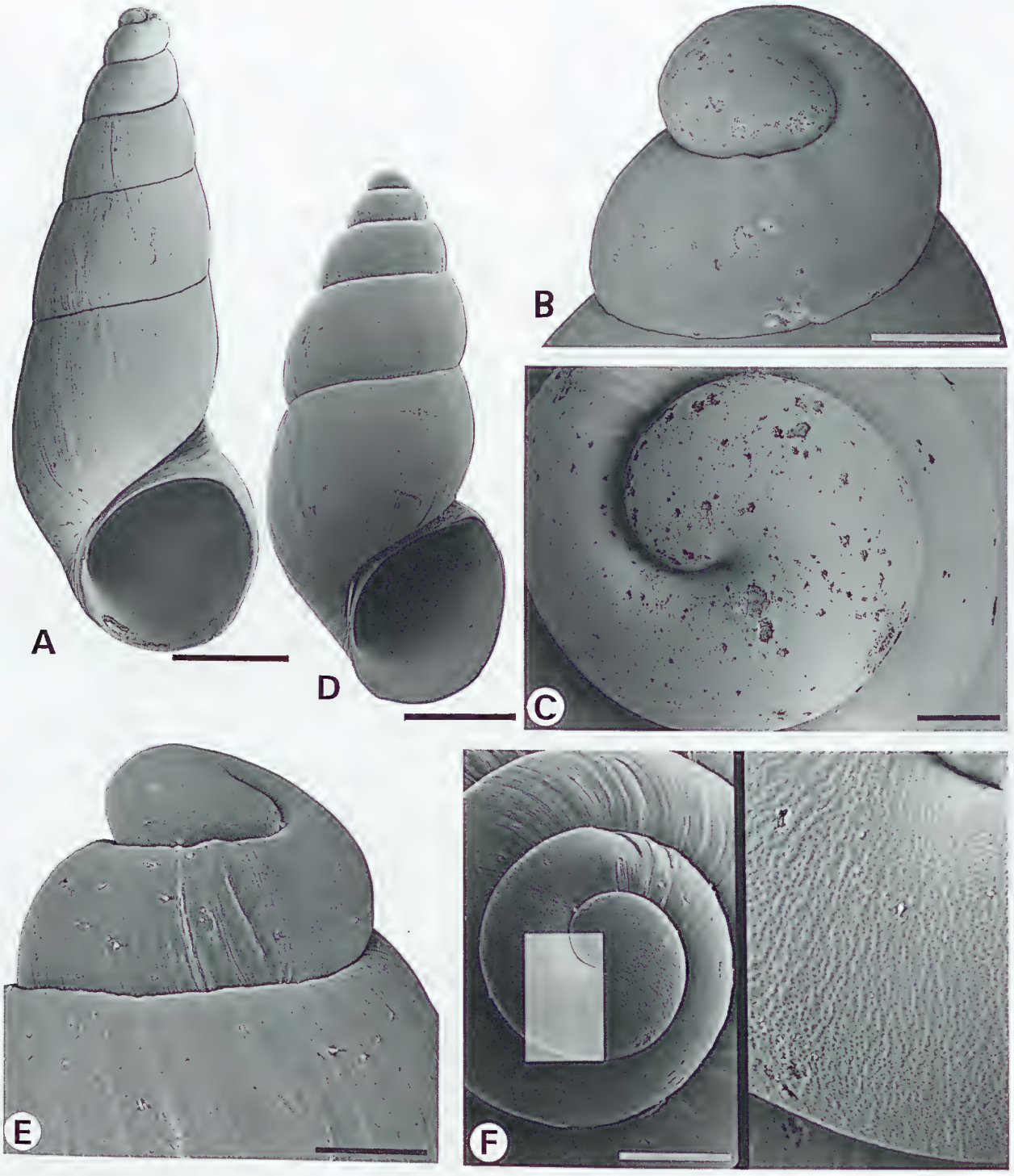


**Fig.23.** Shells of *Jardinella acuminata* n.sp. and *J. zeidlerorum* n.sp. A–C, *J. acuminata*, Stn 73(A); A, shell; B,C, lateral (B) and dorsal (C) views of protoconch; D–F, *J. zeidlerorum*, Stn Z12; D, shell; E,F, lateral (E) and dorsal (F) views of protoconch. The highlighted area in F is magnified a further 4X in the adjacent figure to show the microsculpture. Scales:- A,D – 0.5 mm, B,E,F – 0.1 mm, C – 0.05 mm.

glandular layer to left of ctenidium and near anus. Rectum without arch, anus distant from mantle edge. Kidney not extending forward into pallial roof.

*Male reproductive system* (Figs 21F, 22D): penial lobe(s) absent, distal portion tapering; middle section of penis and most of distal section dark grey to black; base with scattered black spots and grey proximal basal fold; distal end unpigmented. Vas deferens straight or undulating with one to few loops/coils anterior to prostate gland.

*Female reproductive system* (Fig. 22E,F): pallial oviduct with unmodified, rather wide ventral channel, with pallial opening ventroterminal. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is smaller than, albumen gland. Coiled oviduct and bursal duct fused to form common duct about halfway to posterior pallial wall from seminal receptacle duct. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

**Remarks.** This species is similar to the last but has about an extra half whorl (about 4 compared with about 3.5), less convex whorls and a relatively narrower spire (length/width ratio about 1.8 compared with about 2.1). Shell length, aperture length, body whorl length, number of teleoconch whorls, convexity, spire angle, aperture angle, protoconch diameter, and the position of the opercular nucleus all differ significantly (P equal to or less than 0.001).

The female genital system differs from that of *J. jesswiseae* n.sp. in having a thin-walled, unmodified ventral channel and the albumen gland is relatively larger, being only slightly shorter than the capsule gland (less than half the length of the capsule gland in *J. jesswiseae*). The uniformly tapering distal end of the penis differs from that of *J. jesswiseae* which has a short papilla, and the pigmented part of the penis is located much nearer to the distal end in *J. jesswiseae* than in *J. zeidlerorum*.

This species lives in a spring separated from the perimeter of the main Edgbaston group by about 3.5 km.

**Etymology.** The species is named for Wolfgang

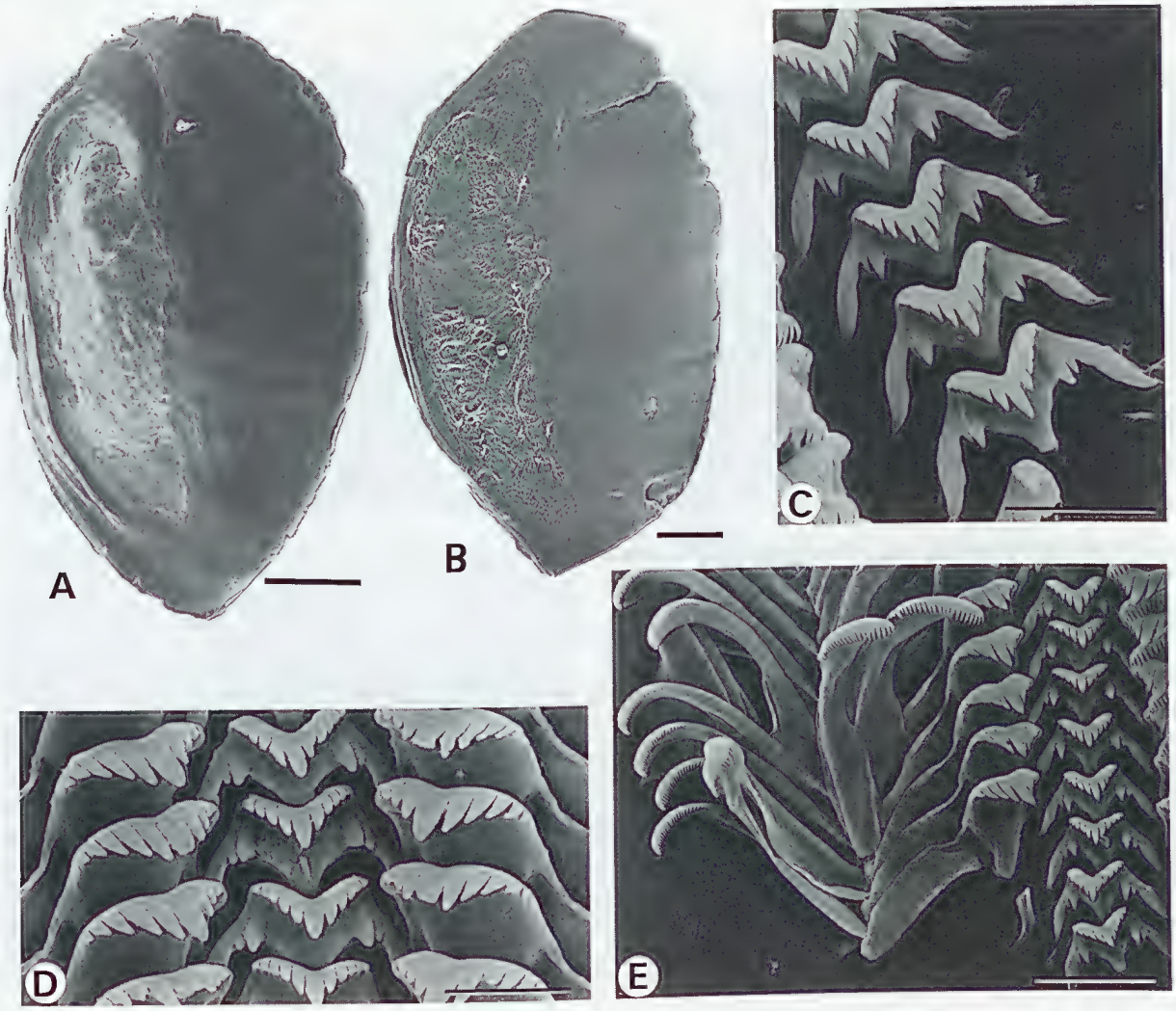


**Fig.24.** *Jardinella acuminata* n.sp. and *Jardinella zeidlerorum* n.sp., opercula and radulae. A,C, *J. acuminata*, Stn 73(A), A, inner side of operculum; C, central teeth of radula; B,D,E, *J. zeidlerorum*, Stn Z12; B, inner side of operculum; D,E, radula, D, detail of central and lateral teeth. Scales:- A,B – 0.2 mm, C,D – 0.01 mm, E – 0.02 mm.

and Lyn Zeidler.

### *Jardinella acuminata* n.sp.

**Localities.** Stn 73, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 433. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow. Stn Z9, "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 73(B) C.156745 (holotype), C.156746 (100 paratypes), Stn 73(A) C.156747 (310 paratypes), SAM Stn Z9(A) D.18542 (4 paratypes), Stn Z9(B) D.18543 (100+ paratypes), QM Stn 73(A) MO.20082 (5 paratypes).

**Diagnosis.** Shell elongate conic, of medium size (up to 3.6 mm in length), smooth, non-umbilicate. Penis without lobe(s), distal part pigmented and tapering, terminal part unpigmented. Pallial oviduct with unmodified ventral channel, opening subterminal and ventral.

**Description.** *Shell* (Figs 16E, 23A–C): very elongate conic, of medium size, 2.29-3.58 mm in length [mean 2.91 (M), 3.00 (F)]; 0.96-1.29 mm in width [mean 1.12 (M), 1.15 (F)]; not sexually dimorphic in size (P greater than 0.4); thin, fragile, translucent white, with indistinct, transparent periostracum. Spire angle 31.51-43.38° [mean 36.75 (M), 36.40 (F)]. Protoconch (Fig. 23B,C), strongly deviated; of 1.3-1.5 whorls [mean 1.39 (M), 1.40 (F)]. Teleoconch of 4.25-5.75 convex whorls [mean 5.00 (M), 4.92 (F)]. Convexity ratio 0.06-0.14 [mean 0.09 (M), 0.09 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.26-0.32 [mean 0.29 (M), 0.28 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 2.47-9.84° [mean 6.31 (M), 5.16 (F)]. Umbilicus closed.

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 3.36 mm, width 1.21 mm, length of aperture 0.89 mm, number of teleoconch whorls 5.50.

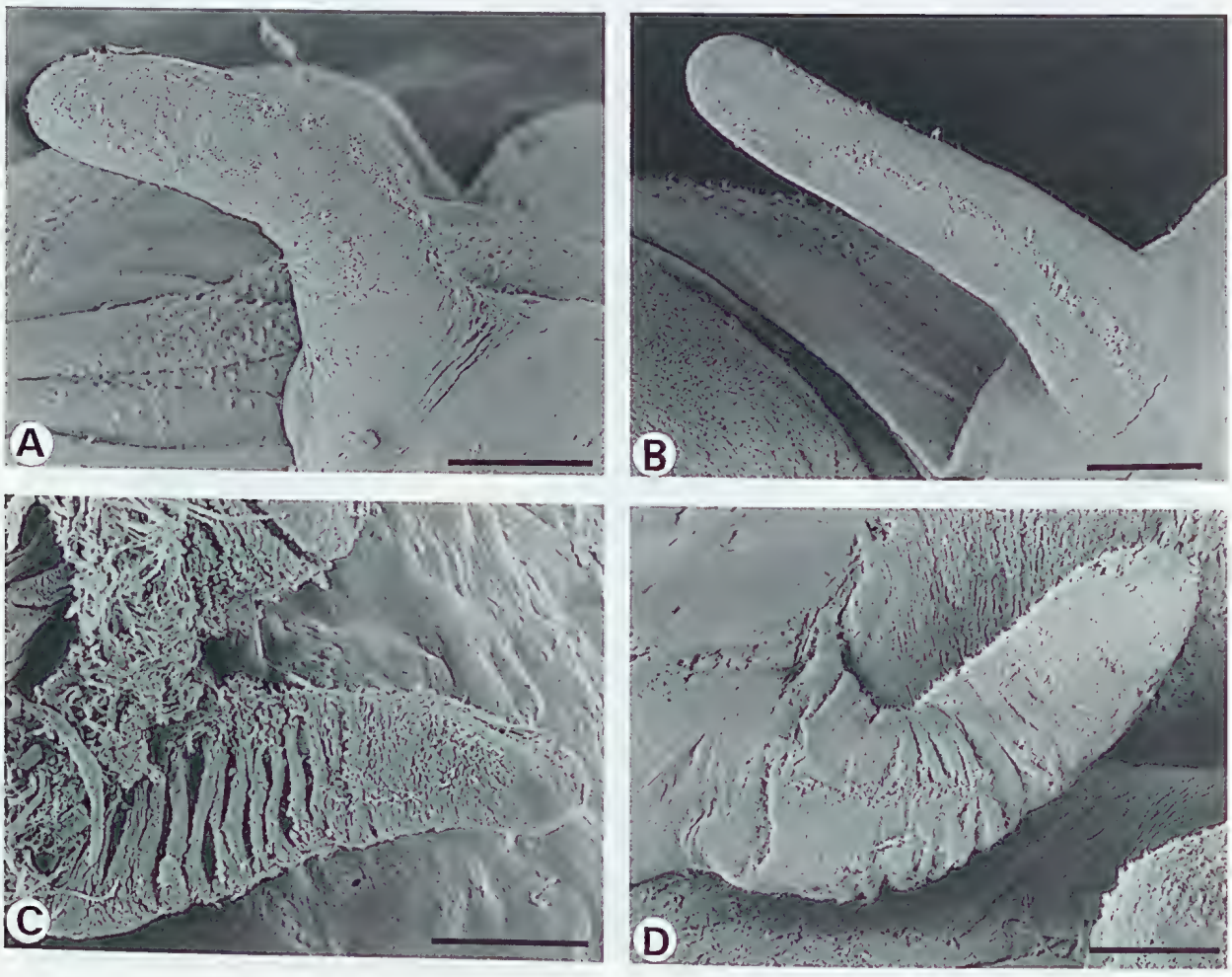


**Fig.25.** Scanning electron micrographs of critically point dried cephalic tentacles of species of *Jardinella*. A,B, *J. eulo*, Stn 11; A, dorsal view of right tentacle; B, ventral view of right tentacle; C, *J. acuminata*, Stn 73(B); ventral view of left tentacle; D, *J. isolata*, Stn 21(C); ventral view of left tentacle. Scales:- A,B,D – 0.1 mm, C – 0.05 mm.

*Operculum* (Fig. 24A): thin, very pale yellow, 0.58-0.81 mm in length [mean 0.69 (M), 0.73 (F)]. With white smear 0.15-0.41 mm in length [mean 0.33 (M), 0.34 (F)]. Ratio of opercular length to position of nucleus 3.52-5.82 [mean 4.46 (M), 4.35 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 24C): each central tooth with 5 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.4-1.5; 2 pairs of basal denticles; dorsal edge inverted U-shaped; basal process long, tongue shaped. Each lateral tooth with cusp formula 3-4.1.3-4; ratio of length of primary cusp/length of adjacent outer cusps 1.8-2; with small basal bulge; outer shaft 1.3-1.7 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Fig. 25C) triangular in section, with no dorsal ciliated band on left tentacle, 1 on right; 2 ventral longitudinal ciliated bands on right tentacle, 1 band medial, 1 (weak) posterior. Head mostly black, pigment extending to, and covering eyes; cephalic tentacles with median black stripe developed to greater or lesser extent. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 26-27 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. Well-developed glandular pad to left of ctenidium, and near anus. Rectum without arch, anus distant from mantle edge. Kidney extends forward slightly into pallial roof.

*Male reproductive system* (Fig. 21D, 22G): penial lobe(s) absent, distal portion tapering; penis with grey area proximal to base of terminal part. Vas deferens with 1 to several loops/coils anterior to prostate gland.

*Female reproductive system* (Fig. 22H,I): pallial oviduct with unmodified ventral channel with ventral, slit-like pallial opening located subterminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is subequal in size to, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

**Remarks.** This species lives in the outflow of Big Spring (Stn 73) (see Table 4), one of the Edgbaston springs, and is distinguished from all others in the genus by its large, elongate shell and straight-sided spire. The only other species with similar shell features (confirmed by discriminate analysis) is *J. zeidlerorum* n.sp., the shell of which differs in its slightly convex spire outline and more convex whorls. Statistical comparison of the measurement data for these two species showed that they differ (P equal to or less than 0.001) in shell length and width, aperture length, convexity, spire angle, number of protoconch and teleoconch whorls, opercular length and position of the opercular nucleus.

A thick glandular pad to the left of the ctenidium (Fig. 4B, gp1) and another in front of the anus (Fig. 4B, gp2) are autapomorphies of *J. acuminata*. Homologous, but thinly developed, pads of epithelial glands are apparent in the same areas in *J. zeidlerorum* and are have been scored as the same character in the phylogenetic analysis. None of the other species show any special development of epithelial glands in these areas.

The genital systems of *J. acuminata* and *J. zeidlerorum* are similar, the male genitalia differing in pigmentation details and in the vas deferens being more looped in *J. acuminata*.

**Etymology.** The specific name is based on the Latin word *acumen* meaning sharp point.

### *Jardinella* sp.

**Locality.** 73(D), "Big Spring" about 3 km south-east of "Edgbaston" homestead, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WFP and PHC, 26 Sept. 1984. Head of large spring with outflow about 170 m.

**Material examined.** AMS Stn 73(D) C.157167.

**Remarks.** A single empty shell (Fig. 26) was found and is not named although it almost certainly represents an additional species. It probably lives in a specialised microhabitat in the head of the spring.

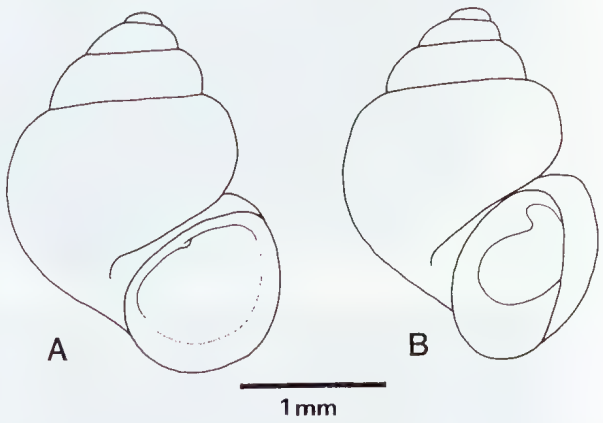


**Fig.26.** A,B, shell of *Jardinella* sp., Stn 73(D), B, rotated slightly to show the columellar fold.

This specimen (length 2.44 mm, width 1.86 mm, length of aperture 1.08 mm, number of teleoconch whorls 3.25) differs from all of the other species in the genus in possessing a prominent columellar fold (Fig. 26B).

## Species from the Springsure Supergroup

### *Jardinella carnarvonensis* n.sp.

**Localities.** Stn Z15, unnamed spring about 5 km north-west of Rangers HQ, just north of 13th river crossing, Carnarvon Gorge National Park, 25°02'30"S 148°11'20"E. Eddystone 619 229. WZ, 8 May 1988. Stn Z16, small seep from rock face east side of Kooraminya

Creek, about 200 m up gorge, about 7.3 km west of Rangers HQ, Carnarvon Gorge National Park, 25°02'20"S 148°11'E. Eddystone 619 229. WZ, 8 May 1988. Stn Z17, unnamed side spring, about 300 m up Hellhole Gorge (Koolaro Creek), about 3 km west of Rangers HQ, Carnarvon Gorge National Park,

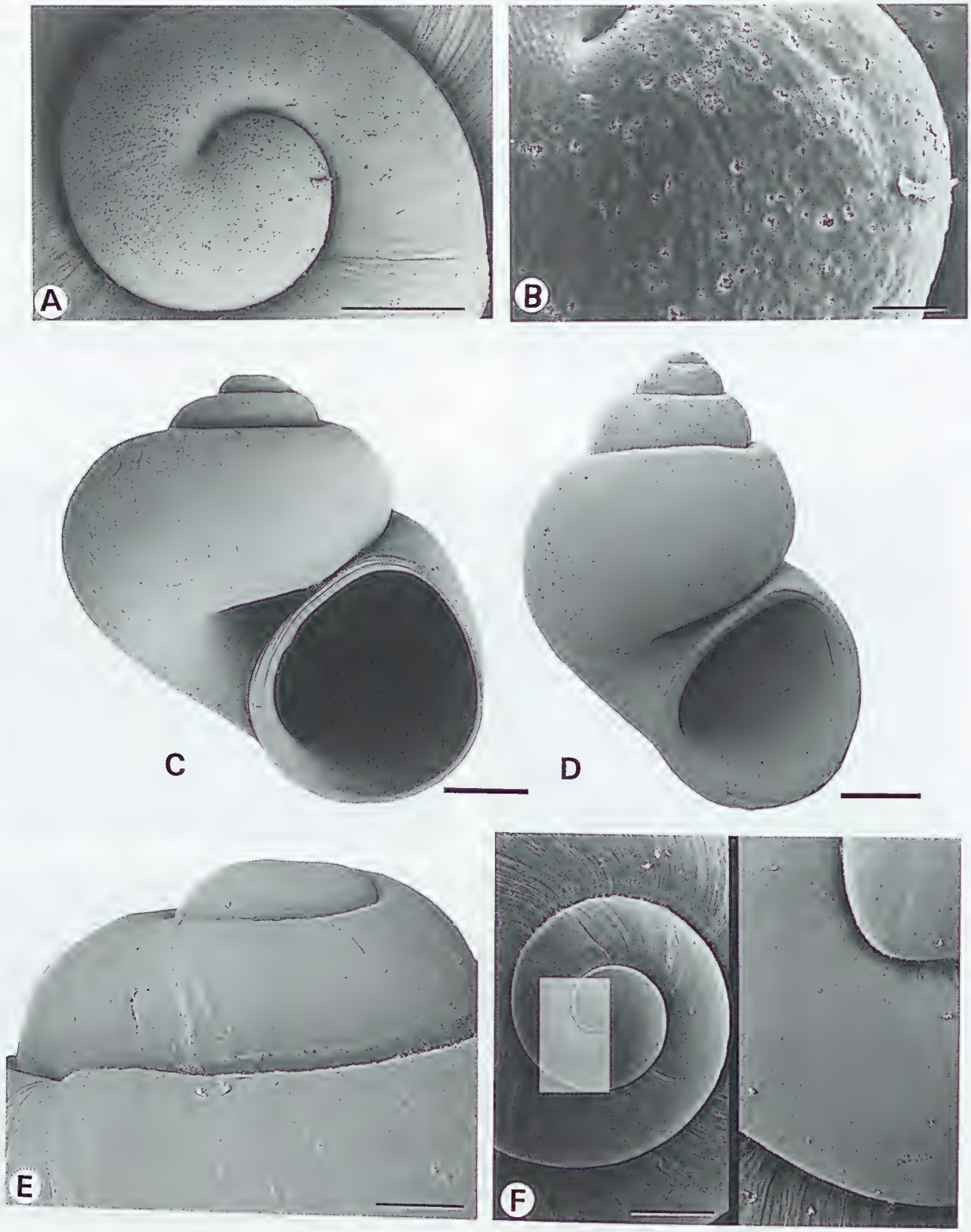


**Fig.27.** Shells of *Jardinella exigua* n.sp. and *J. carnarvonensis* n.sp. A–C, *J. exigua*, Stn 89; A,B, dorsal view of protoconch (A) and detail of microsculpture (B); C, shell; D–F, *J. carnarvonensis*, Stn Z15; D, shell; E,F, lateral (E) and dorsal (F) views of protoconch. The highlighted area in F is magnified a further 4X in the adjacent figure to show the microsculpture. Scales:- A,E – 0.1 mm, B – 0.02 mm, C – 0.3 mm, D – 0.5 mm, F – 0.2 mm.

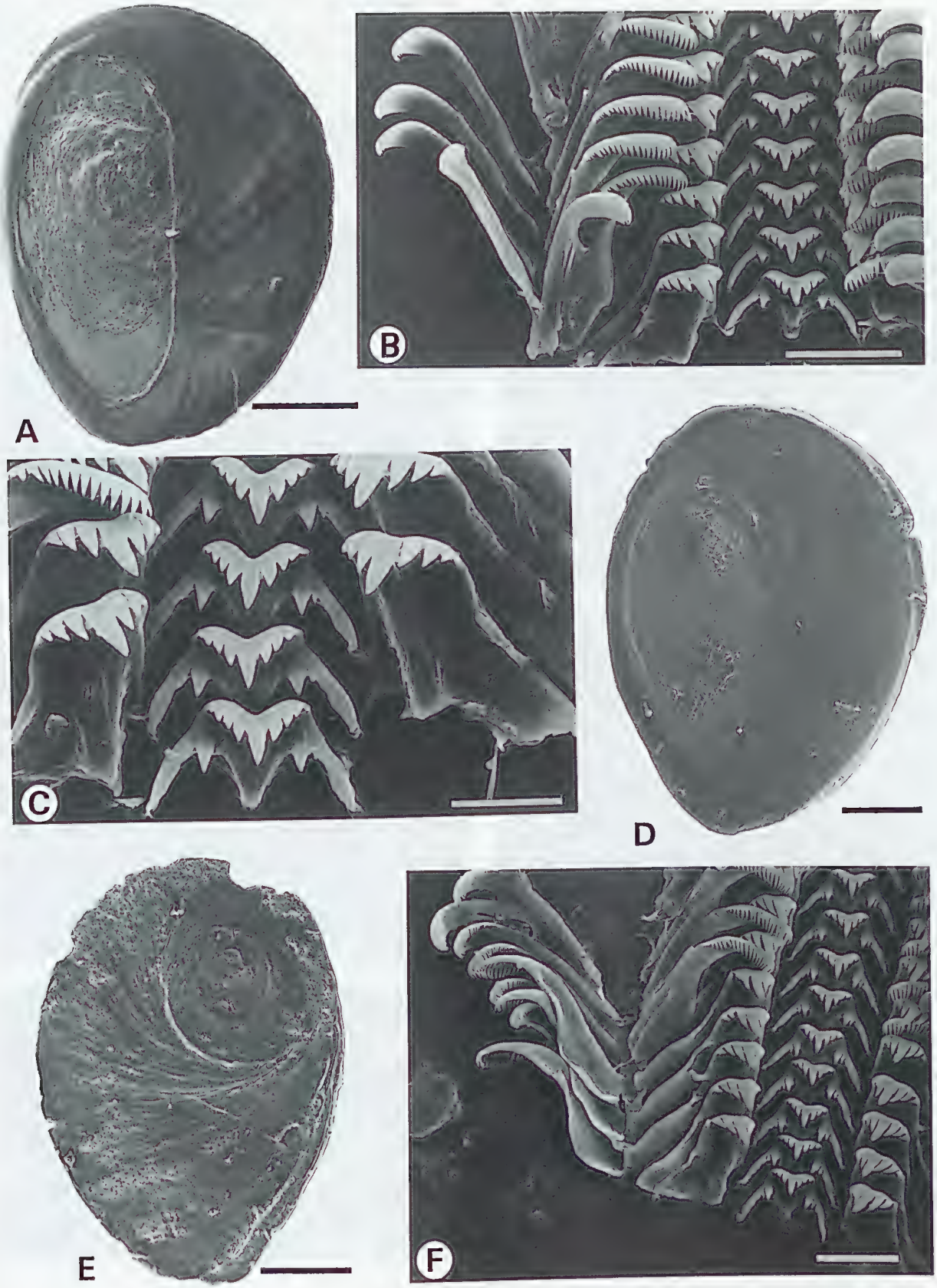


**Fig.28.** *Jardinella exigua* n.sp. and *J. carnarvonensis* n.sp., opercula and radulae. A–C, *J. exigua*, Stn 89, A, inner side of operculum; B,C, radula, C, detail of central and lateral teeth of radula; D–F, *J. carnarvonensis*, Stn Z15; D,E, inner (D) and outer (E) sides of operculum; F, radula. Scales:- A,D,E – 0.2 mm, B – 0.01 mm, C,F – 0.02 mm.

25°03'30"S 148°12'30"E. Eddystone 622 228. WZ, 8 May 1988.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn Z15 C.156786 (holotype), Stn Z15 C.156787 (14 paratypes), Stn Z16 C.156788 (5 paratypes), Stn Z17 C.156789 (5 paratypes), SAM Stn Z15 D.18544 (80+ paratypes), Stn Z16 D.18545 (50+ paratypes), Stn Z17 D.18546 (50+ paratypes), QM Stn Z15 MO.20083 (2 paratypes).

**Diagnosis.** Shell trochiform, small (up to 2.5 mm in length), smooth, umbilicate. Penis with expanded, pigmented distal end and small, terminal papilla. Pallial oviduct with wide vestibule, pallial opening terminal and ventral.

**Description.** *Shell* (Figs 6D, 27D–F): trochiform, small to medium size, 1.8-2.53 mm in length [mean 2.06 (M), 2.14 (F)]; 1.57-2.13 mm in width [mean 1.81 (M), 1.90 (F)]; not

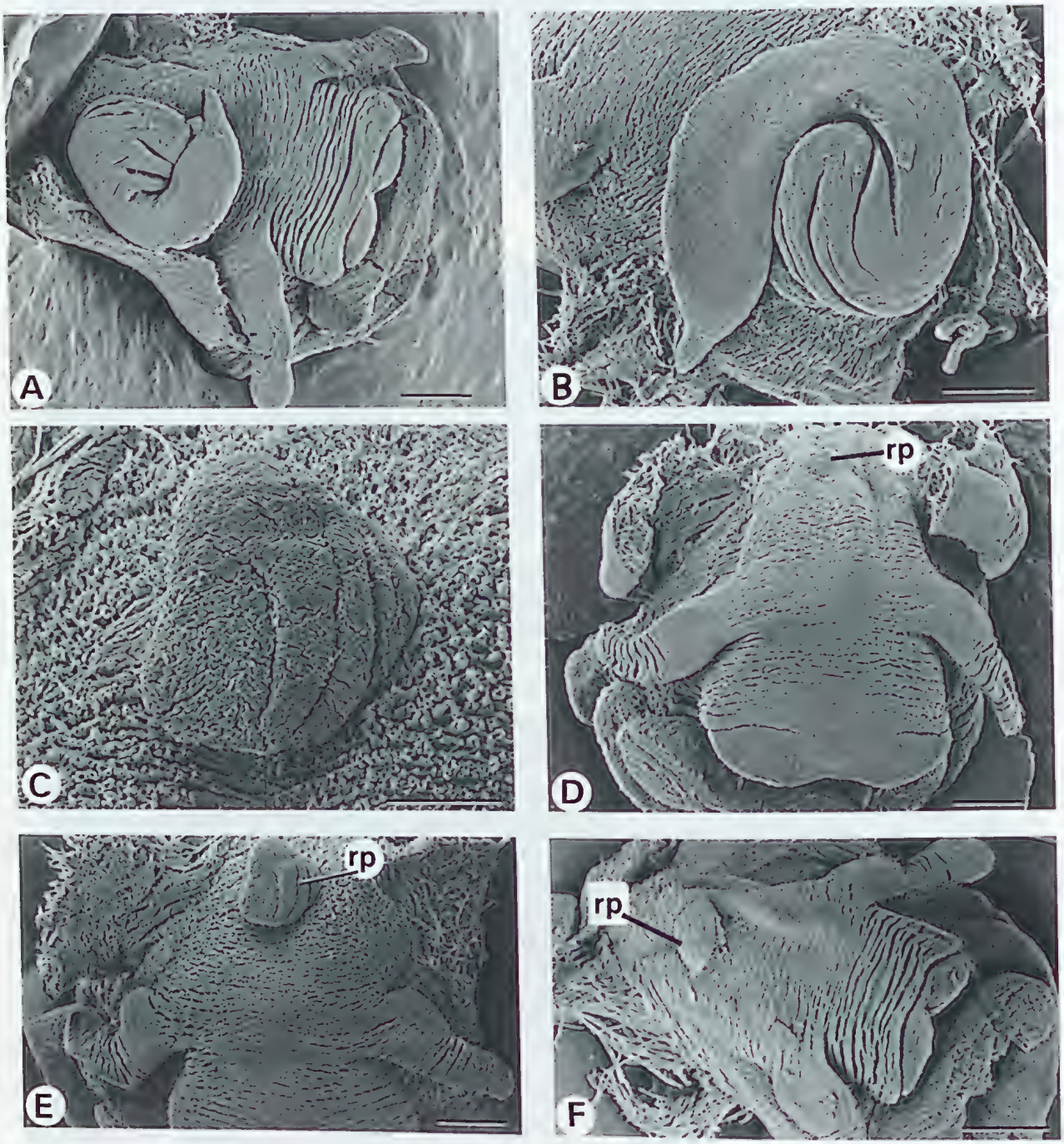


**Fig.29.** Scanning electron micrographs of critically point dried penes and rudimentary penes of species of *Jardinella*. A,F, *J. exigua*, Stn 93(A); A, penis; F, head of female with rudimentary penis; B–E, *J. carnarvonensis*, Stn Z15; B, penis; C–E, rudimentary penis in females; D,E, dorsal view of head and neck with rudimentary penis (rp) on neck, C, detail of the rudimentary penis of the specimen shown in E. rp – rudimentary penis. Scales:- A,B,D-F – 0.1 mm, C – 0.05 mm.

sexually dimorphic in size (P greater than 0.05); of medium thickness, translucent to opaque white, with indistinct, pale yellowish brown periostracum. Spire angle 80.62-112.68° [mean 95.31 (M), 93.87 (F)]. Protoconch (Fig. 27E,F) of 1.2-1.3 whorls [mean 1.24 (M), 1.25 (F)]. Teleoconch of 2.3-2.9 convex whorls [mean 2.51 (M), 2.57 (F)]. Convexity ratio 0.16-0.33 [mean 0.25 (M), 0.25 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.49-0.61 [mean 0.55 (M), 0.54 (F)]. Inner lip of medium thickness, of medium width. Outer lip prosocline, angle 22.82- 40.19° [mean 30.52 (M), 31.43 (F)]. Umbilicus of medium width [0.13-0.36 mm in width; mean 0.25 (M), 0.25 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 2.25 mm, width 1.94 mm, length of aperture 1.25, number of teleoconch whorls 2.50.

*Operculum* (Fig. 28D,E): thin, yellow, 0.81-1.19 mm in length [mean 0.97 (M), 1.01 (F)]. Without white smear. Ratio of opercular length to position of nucleus 2.6-3.66 [mean 3.04 (M), 3.12 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 28F): each central tooth with 3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.6-1.8; 2-3 pairs of basal denticles; dorsal edge concave; basal process long, tongue shaped. Each lateral tooth with cusp formula 3.1.3; ratio of length of primary cusp/length of adjacent outer cusps 1.4-1.5; basal bulge absent; outer shaft 1.8-2.1 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Figs 9D, 29D,E) triangular in section, with no dorsal ciliated bands present; scattered ventral cilia only. Degree of pigmentation variable, snout with grey to black sides, mid-dorsal stripe and distal end

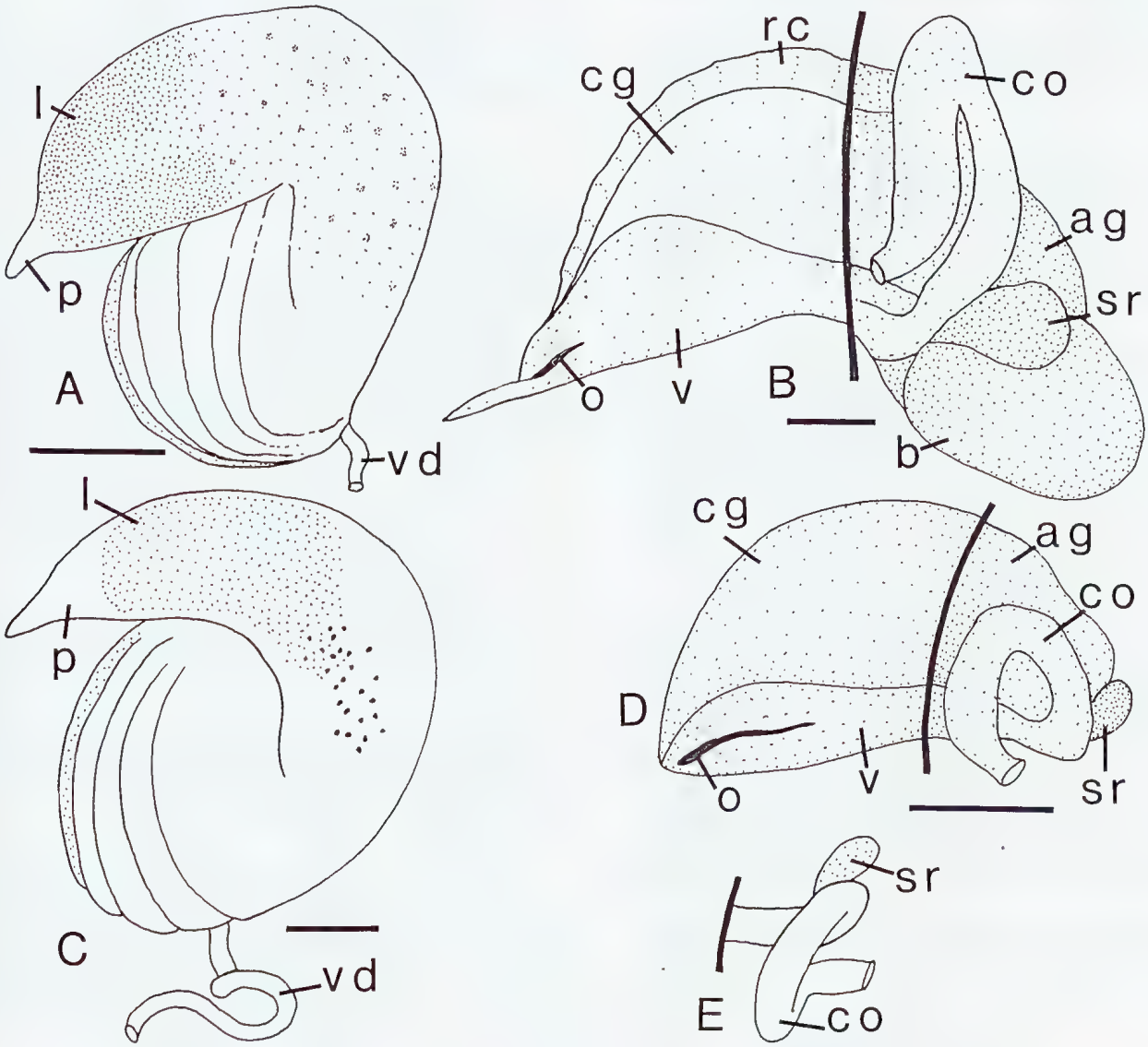


**Fig.30.** Genitalia of species of *Jardinella*. A,B, *J. exigua*, Stn 89, A, penis, B, oviduct; C–E, *J. carnarvonensis*, Stn Z15, C, penis, D,E, oviduct. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:- A,D – 0.2 mm, B,C – 0.1 mm.

unpigmented; black patch behind each eye; cephalic tentacles grey to black dorsally; foot pale to dark grey. Visceral coil pigmentation mostly black or dark grey.

**Anatomy:** *Mantle cavity:* ctenidium with 15-19 filaments; apex on right, or towards centre. Osphradium near middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with prominent arch, anus near mantle edge. Kidney not extending forward into pallial roof.

*Male reproductive system* (Figs 29B, 30C): penial lobe(s) absent but smooth distal part expanded (swollen); distal end of penis with very short papilla; distally penis (except for papilla) black or grey, with few grey spots in middle section and grey proximal basal lobe, rest unpigmented. Vas deferens with few loops/coils on anterior end of prostate gland and additional loops/coils anterior to prostate gland.

*Female reproductive system* (Fig. 30D,E): pallial oviduct with ventral channel modified as wide, muscular vestibule, ventral pallial opening short slit located terminally. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from middle of anterior side of ovate bursa copulatrix which lies posterior to, and is slightly smaller than, albumen gland. Coiled oviduct and bursal duct separate to posterior pallial wall. Coiled oviduct simple U-shape. Rudimentary penis present in most or all females (Fig. 29C–E).

**Remarks.** This species is similar in shell shape to *J. coreena* n.sp. but is smaller in size [all teleoconch characters, including shell length and width (but excluding convexity) are significantly different (P less than 0.001)]. Comparing the generalised distances between the species generated by discriminate analysis on shell characters this species is most similar to *J. coreena*, and also similar to *J. exigua* n.sp. (Table 5). The Euclidean distances, show this species having most similarity with *J. colmani* n.sp. (Table 6).

The springs in Carnarvon Gorge flow from sandstones that are part of the same series making up the aquifer of the Great Artesian Basin. The water flowing from them, however, is not derived from the Great Artesian Basin (M.A. Habermehl, personal communication). They flow into Carnarvon Creek, a tributary of the Brown River, a tributary of the Fitzroy River. This river has an eastern drainage, unlike all of the other drainages with which the springs are associated which are west of the Great Divide.

**Etymology.** The species is named for Carnarvon Gorge.

### *Jardinella exigua* n.sp.

**Localities.** Stn 88, small unnamed spring on hillside about 2.5 km north-west of "Dooloogarah" homestead, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984. Stn 89, small unnamed spring on hillside about 100 m south-east of Stn 88, about 2.5 km north-west of "Dooloogarah" homestead, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984. Head of spring fenced off and a small pipe leading from it. Stn 93, small seep about 1.2 km north-east of "Dooloogarah" homestead, south of Carnarvon Gorge National Park, 24°52'S 147°48'E. Springsure 581 249. WFP and PHC, 1 Oct. 1984. With small pipe leading from it. A – head of spring; B – outflow.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 93(B) C.156781 (holotype), C.156782 (200+ paratypes), Stn 93(A) C.156785 (100+ paratypes), Stn 88 C.156783 (500+ paratypes), Stn 89 C.156784 (500+ paratypes), SAM Stn 88 D.18547 (20 paratypes), QM Stn 88 MO.20084 (5 paratypes).

**Diagnosis.** Shell trochiform, small (up to 1.7 mm in length), smooth, umbilicate. Penis with slightly tapering distal end and short, terminal papilla; middle part of distal half pigmented. Pallial oviduct with unmodified ventral channel, ventral pallial opening slit-like and subterminal.

**Description.** *Shell* (Figs 6E, 27A–C): trochiform, small, 1.21-1.68 mm in length [mean 1.45 (M), 1.38 (F)]; 1.29-1.67 mm in width [mean 1.52 (M), 1.46 (F)]; not sexually dimorphic in size (P greater than 0.08); thin, fragile, translucent white, with indistinct, very pale orange brown to colourless periostracum. Spire angle 82.96-118.28° [mean 103.68 (M), 105.04 (F)]. Protoconch (Fig. 27A,B) of 1.2-1.4 whorls [mean 1.26 (M), 1.27 (F)]. Teleoconch of 1.6-2.2 convex whorls [mean 1.87 (M), 1.93 (F)]. Convexity ratio 0.18-0.37 [mean 0.26 (M), 0.26 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.53-0.69 [mean 0.62 (M), 0.61 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 21.35-36.35° [mean 27.47 (M), 29.58 (F)]. Umbilicus of medium width [0.16-0.31 mm in width; mean 0.27 (M), 0.25 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 1.52 mm, width 1.65 mm, length of aperture 0.98 mm, number of teleoconch whorls 2.00.

*Operculum* (Fig. 28A): thin, very pale yellow, 0.7-0.92 mm in length [mean 0.83 (M), 0.80 (F)]. Without white smear. Ratio of opercular length to position of nucleus 2.26-3.52 [mean 2.97 (M), 2.85 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 28B,C): each central tooth with 3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.5-1.7; 2 pairs of basal denticles; dorsal edge concave; basal process long, tongue shaped. Each lateral tooth with cusp formula 3.1.3; ratio of length of primary cusp/length of adjacent outer cusps 1.7-2; with small basal bulge; outer shaft 1.7-1.8 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Figs 9B, 29A,F) triangular in section, with no dorsal ciliated bands present; distinct ciliated band along most of ventral surface. Unpigmented except for variable sized dark grey to black patch behind eyes continuous with small patches on sides of snout; sides of foot and opercular lobes sometimes grey. Visceral coil

pigmentation variable, mostly with black or dark grey dorsally.

**Anatomy.** *Mantle cavity:* ctenidium with 11-17 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with prominent arch, anus near mantle edge. Kidney extending well forward into pallial roof.

*Male reproductive system* (Figs 29A, 30A): penial lobe(s) absent; distal end of penis with short papilla; distal third of penis pale grey, last basal fold pale grey, rest unpigmented. Pallial vas deferens with many loops/coils which lie over anterior end of prostate gland.

*Female reproductive system* (Fig. 30B): pallial oviduct with unmodified ventral channel; opening slit-like, commences subterminally and extends to a little over half length of pallial ventral channel. Seminal receptacle lies at posterior edge of albumen gland. Bursa copulatrix and its duct absent. Coiled oviduct simple U-shape. Rudimentary penis present in almost all females (Fig. 29F).

**Remarks.** The long, slit-like oviducal opening and absence of a bursa copulatrix are important characters which separate this species from the last, with which it is generally most similar. These characters could be considered to be of generic significance except that this species probably shares a common ancestor with *J. carnarvonensis* n.sp., that species having most characters in common, including a slit-like (but shorter) oviducal opening. Both species also have a rudimentary penis in females (Fig. 29C–F).

These two species can be distinguished using shell characters by the larger size of *J. carnarvonensis*, shell length and shell width both being significantly different (P less than 0.001), as are aperture length and width, length of body whorl, spire angle, protoconch diameter, teleoconch whorls, opercular length and the position of the opercular nucleus. Generalised distances between the species generated by discriminate analysis show this species to be most similar to *J. carnarvonensis* (Table 5), but the Euclidean distances between the groups show, as with *J. carnarvonensis*, that *J. colmani* n.sp. is the most similar species (Table 6).

The shell of this species is somewhat similar to that of species of *Trochidrobia* but they lack a seminal receptacle, have a simple penis, a more subcentral opercular nucleus, a radula with more numerous cusps on the central and lateral teeth and 1-2 basal denticles on the central teeth.

The small springs in which this species lives flow from Tertiary basalts and are thus not derived from the Great Artesian Basin.

**Etymology.** The specific name is from the Latin word *exiguus(a)* meaning small.

## Species from the Springvale Supergroup

### *Jardinella isolata* n.sp.

**Localities.** Stn 21, Elizabeth Springs about 26 km north-north-west of Springvale, 23°20'30"S 140°34'40"E. Springvale 457 418. WFP and PHC, 10 Sept. 1984. A – top of spring; B – outflow; C – large seep; D – small seeping pool on side of creek. Stn Z1, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Low mound nearest creek. Stn Z2, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Mound adjacent to spring with old fence about 300 m north of Stn Z1.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 21(C) C.156772 (holotype), C.156773 (500+ paratypes), Stn 21(A) C.156775 (7 paratypes), Stn 21(B) C.156774 (70 paratypes), SAM Stn Z1 D.18548 (50+ paratypes), Stn Z2 D.18549 (50+ paratypes), QM Stn 21(C) MO.20085 (5 paratypes).

**Diagnosis.** Shell conical, medium to large (up to 3.9 mm in length), smooth, umbilicate, last part of body whorl sometimes detached from parietal wall. Penis with pigmented distal lobes and small, terminal papilla. Pallial oviduct with unmodified ventral channel and ventral, terminal pallial opening.

**Description.** *Shell* (Figs 16A, 31C–F): conical, medium to large, 2.67-3.88 mm in length [mean 3.05 (M), 3.23 (F)]; 1.86-2.45 mm in width [mean 2.05 (M), 2.17 (F)]; not sexually dimorphic in size (P greater than 0.1); of medium thickness, translucent white to yellowish white, with indistinct, transparent periostracum. Spire angle 63.01-79.32° [mean 71.11 (M), 70.01 (F)]. Protoconch (Fig. 31D,E) of 1.25-1.35 whorls [mean 1.27 (M), 1.28 (F)]. Teleoconch of 2.5-3.3 convex whorls [mean 2.91 (M), 2.81 (F)]. Convexity ratio 0.15-0.24 [mean 0.19 (M), 0.19 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.43-0.54 [mean 0.49 (M), 0.47 (F)]. Inner lip thin, narrow. Outer lip prosocline, angle 4.34-20.86° [mean 11.13 (M), 13.36 (F)]. Umbilicus medium [0.32-0.71 mm in width; mean 0.41 (M), 0.46 (F)].

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 3.29 mm, width 2.20 mm, length of aperture 1.63 mm, number of teleoconch whorls 2.70.

*Operculum* (Fig. 32D): thin, very pale yellow, 1.28-1.64 mm in length [mean 1.41 (M), 1.46 (F)]. With white smear 0.34-0.74 mm in length [mean 0.52 (M), 0.53 (F)]. Ratio of opercular length to position of nucleus 2.96-3.68 [mean 3.27 (M), 3.26 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 32C): each central tooth with 4 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.8-2; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped. Each lateral tooth with cusp formula 2.1.4; ratio of length of primary cusp/length of

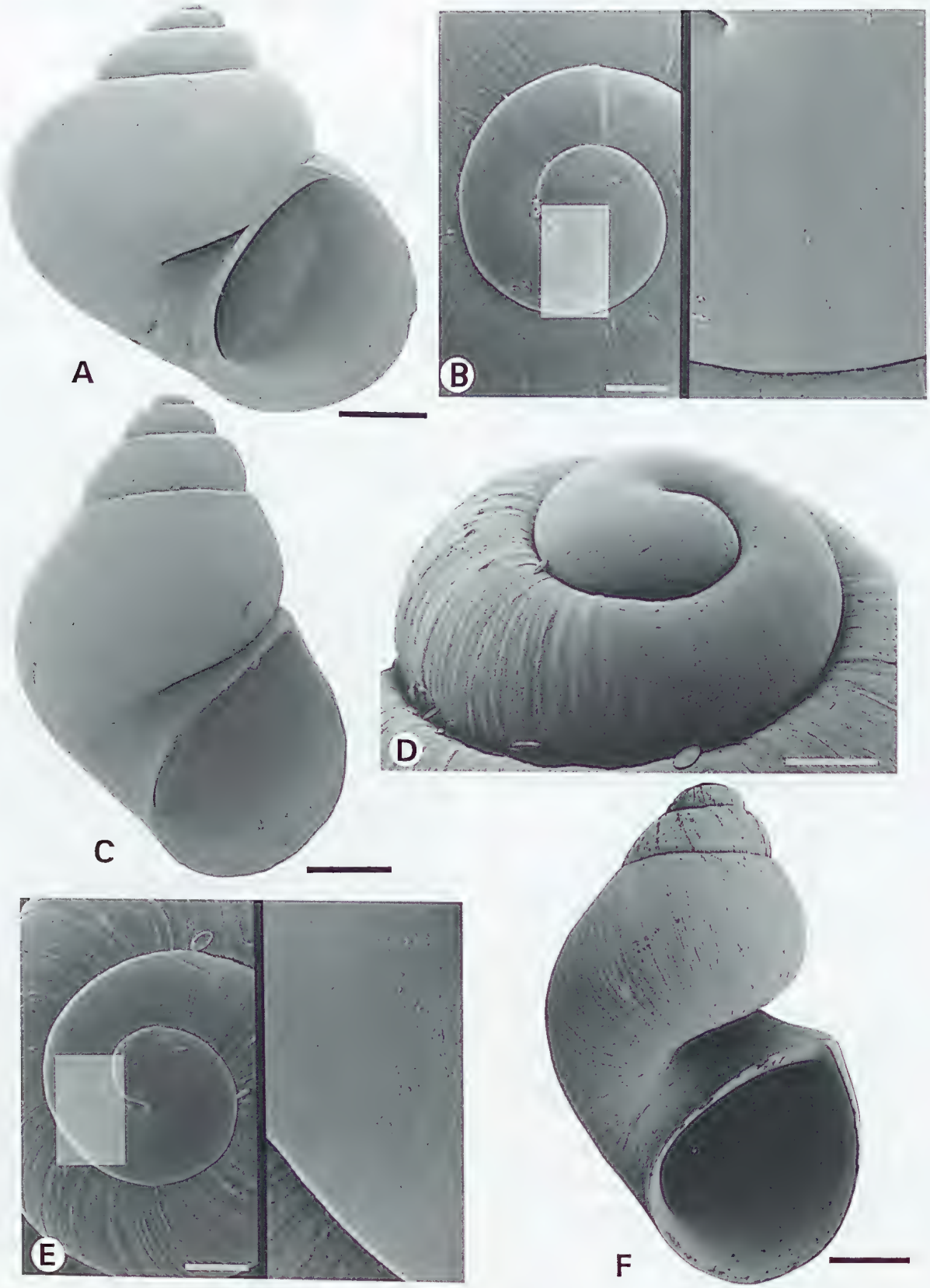


**Fig.31.** Shells of *Jardinella eulo* n.sp. and *J. isolata* n.sp. A,B, *J. eulo*, Stn 11; A, shell; B, dorsal view of protoconch; the highlighted area is magnified a further 4X in the adjacent figure to show the microsculpture. C–F, *J. isolata*, Stn 21(C); C,F, shell; D,E, lateral (D) and dorsal (E) views of protoconch. The highlighted area in E is magnified a further 4X in the adjacent figure to show the microsculpture. Scales:- A,C,F – 0.5 mm, B,D,E – 0.1 mm.

adjacent outer cusps 1.4-1.5; with small basal bulge; outer shaft 1.6-1.8 times longer than cutting edge.

*Head-foot:* cephalic tentacles (Fig. 25D) oval to circular in section, or triangular in section, with dorsal ciliated band present on both tentacles; 2 distinct ciliated bands along most of ventral surface. Head and dorsal snout grey to black; if grey has black patch at base of tentacles behind eyes; unpigmented patch in front of eyes; rest of dorsal surface of cephalic tentacles grey except unpigmented distal end; foot grey to unpigmented. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 24-26 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland moderately to well developed. No glandular pad to left of ctenidium, or near anus. Rectum without arch, anus with intermediate position relative to mantle edge. Kidney not extending forward into pallial roof.

*Male reproductive system* (Figs 33A,B, 34A): penial lobes represented by flattened, expanded portion distally; short papilla terminally; distal half of penis grey, expanded distal area dark grey. Pallial vas deferens straight or undulating.

*Female reproductive system* (Fig. 34B,C): pallial oviduct with unmodified ventral channel. Seminal receptacle lies at anterior edge of bursa. Bursal duct arises from anteroventral side of elongately-ovate

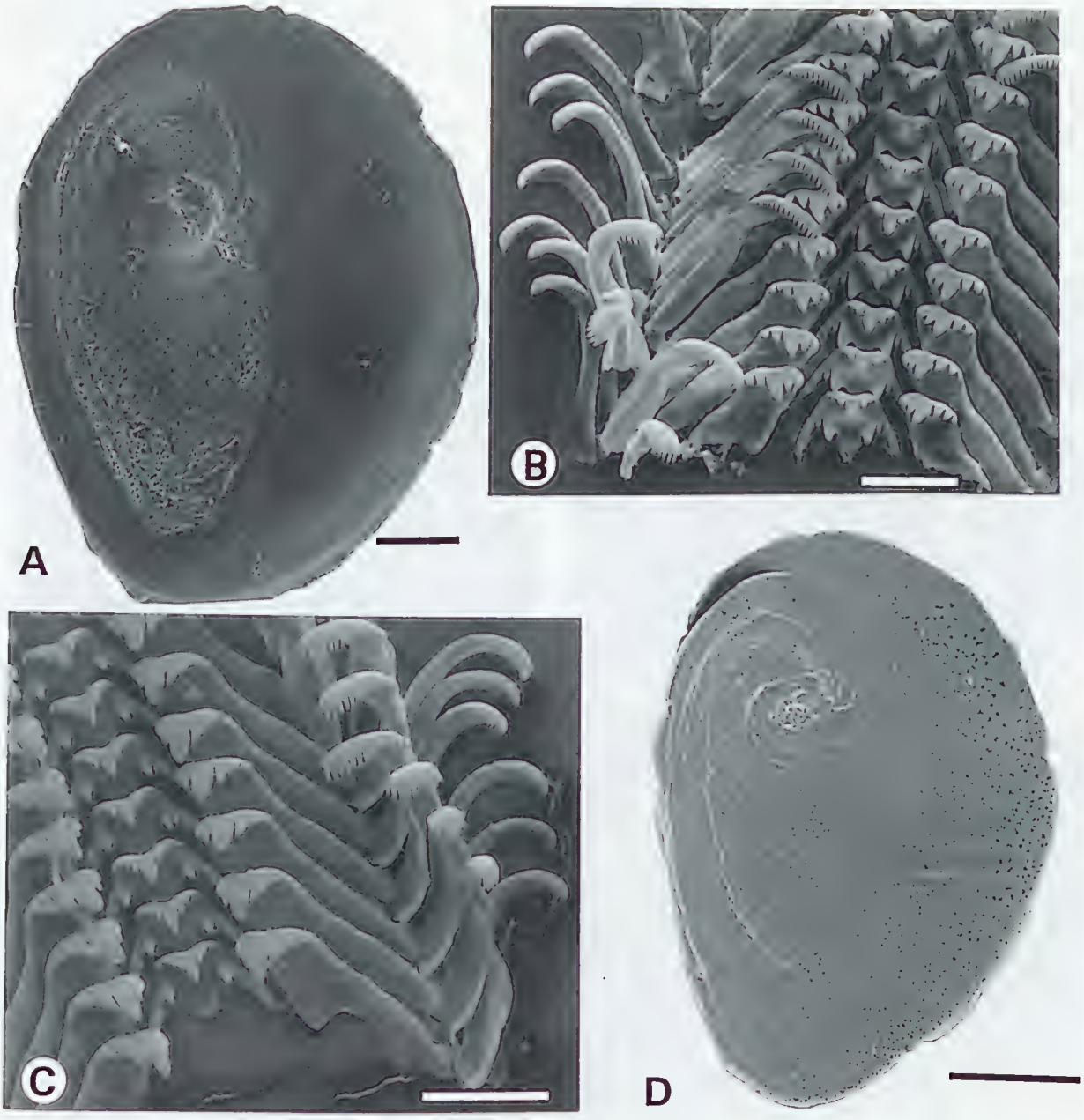


**Fig.32.** *Jardinella eulo* n.sp. and *J. isolata* n.sp., opercula and radulae. A, B, *J. eulo*, Stn 11, A, inner side of operculum; B, radula. C,D, *J. isolata*, Stn 21(C); C, radula; D, inner side of operculum. Scales:- A,D – 0.2 mm, B,C – 0.025 mm.

bursa copulatrix which lies posteroventral to, and is smaller than, albumen gland. Coiled oviduct and bursal duct fused to form common duct just in front of seminal receptacle duct. Coiled oviduct basically U-shaped but with extra bend proximally. Rudimentary penis absent in females.

**Remarks.** This species, like *J. corrugata* n.sp., has a tendency for the aperture to become detached from the parietal wall. It is readily distinguished from all other species of *Jardinella* by its rather large, smooth, broadly conical shell. Discriminate analysis shows that this species is closest to *J. coreena* n.sp. in shell characters but it differs from that species in the more elongate shell and particularly in both male and female genital characters.

The female genital system is similar to that of several other species of *Jardinella* and has a simple ventral channel. The male reproductive system differs in detail in having a simple pallial vas deferens and the penis differs from all other species in detail in having a broad, flattened distal end with a very short papilla.

This species lives in the very isolated Elizabeth Springs in far western Queensland, south-east of Boulia and is the only species living in this area.

**Etymology.** The specific name is taken from the New Latin word *isolatus* meaning detached, separated, based on *solus* (Latin) meaning alone.

## Species from the Eulo Supergroup

### *Jardinella eulo* n.sp.

**Localities.** Stn 8, unnamed spring at Tunga Bore near Mount Tunga, about 43 km west-south-west of Eulo, 28°13'S 144°38'E. Eulo 252 498. WFP and PHC, 6 Sept. 1984. Stn 11, "Rocky Springs" near Mount Francis about 52 km south-west of Eulo, 28°18'S 144°32'E. Eulo 244 489. WFP and PHC, 7 Sept. 1984.

**Material examined.** HOLOTYPE AND PARATYPES – AMS Stn 11 C.156778 (holotype), C.156779 (500+ paratypes), Stn 8 C.156780 (500+ paratypes), SAM Stn 11 D.18550 (20 paratypes), QM Stn 11 MO.20086 (5 paratypes).

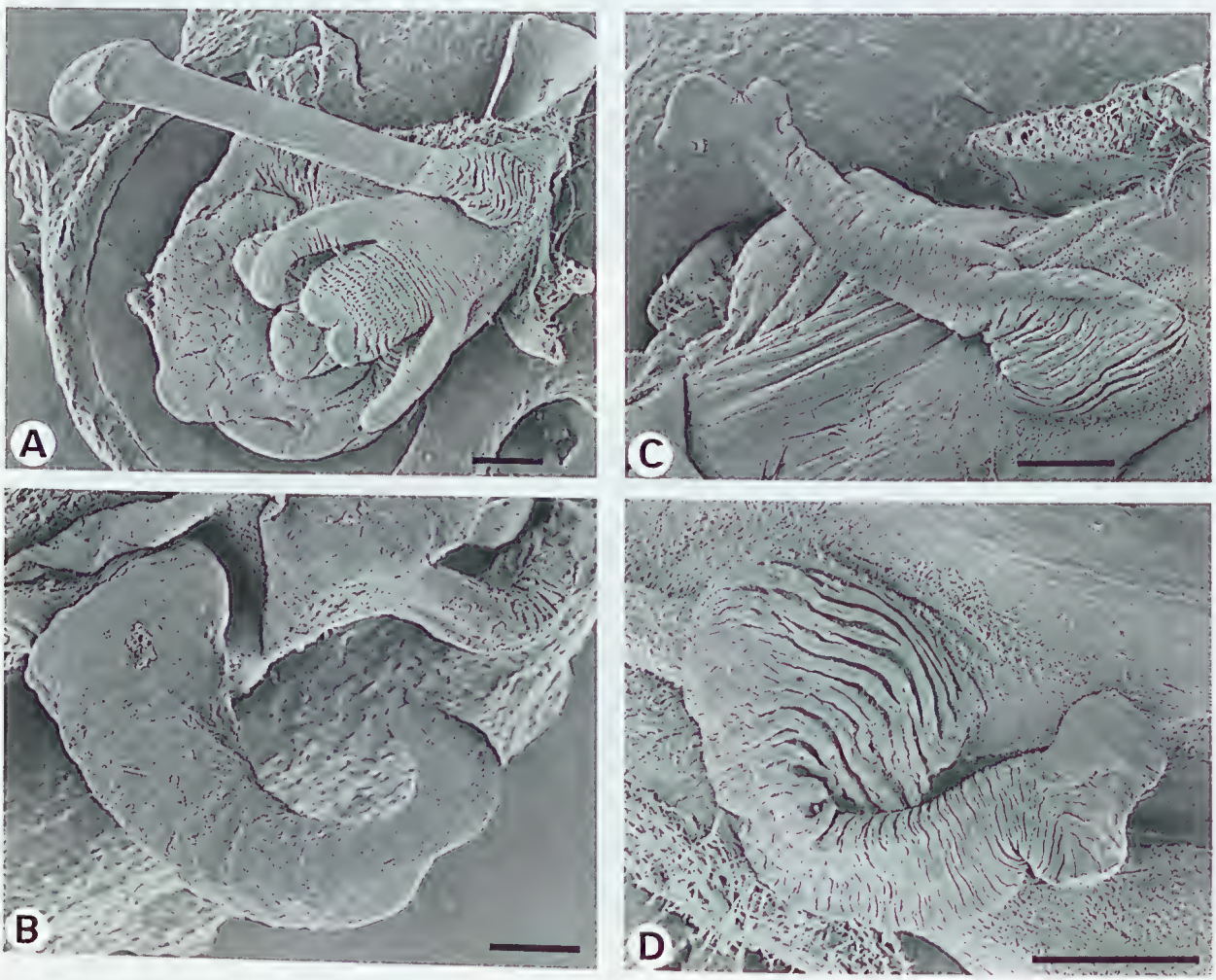


**Fig.33.** Scanning electron micrographs of critically point dried penes of species of *Jardinella*. A,B, *J. isolata*, Stn 21(C), A, penis extended, also showing dorsal view of head-foot; B, penis contracted; C, D, *J. eulo*, Stn 11; C, penis partially extended; D, penis contracted. Scales:- 0.2 mm.

**Diagnosis.** Shell trochiform, of medium size (up to 2.8 mm in length), smooth, umbilicate. Penis with terminal lobes and short, reflected papilla. Pallial oviduct with unmodified ventral channel, pallial opening terminal and ventral. Coiled oviduct extends nearly to posterior end of bursa copulatrix (unlike all other species).

**Description.** *Shell* (Figs 6C, 31A,B): trochiform, of medium size, 2.03-2.84 mm in length [mean 2.36 (M), 2.58 (F)]; 2.19-2.91 mm in width [mean 2.46 (M), 2.75 (F)]; sexually dimorphic in size (P less than 0.03); of medium thickness, translucent orange brown, with indistinct, transparent periostracum. Spire angle 92.01-108.07° [mean 100.29 (M), 99.79 (F)]. Protoconch (Fig. 31B) of 1.25-1.4 whorls [mean 1.29 (M), 1.28 (F)]. Teleoconch of 2.5-3 convex whorls [mean 2.64 (M), 2.73 (F)]. Convexity ratio 0.17-0.24 [mean 0.22 (M), 0.20 (F)]. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.56-0.67 [mean 0.60 (M), 0.63 (F)]. Inner lip of medium thickness, of medium width. Outer lip prosocline, angle 19.57-32.1° [mean 27.94 (M), 24.15 (F)]. Umbilicus medium [0.2-0.53 mm in width; mean 0.34 (M), 0.40 (F)].

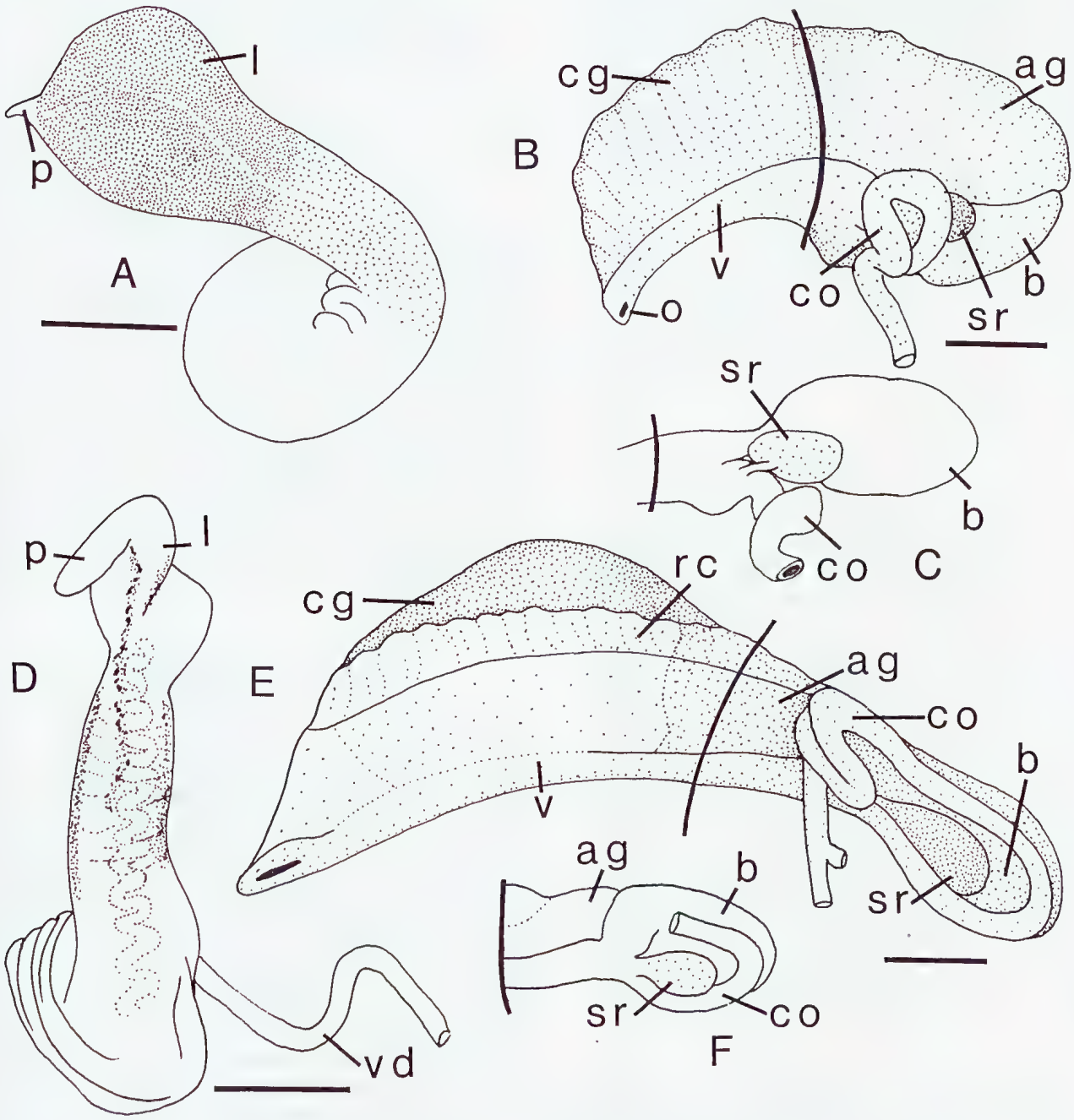


**Fig.34.** Genitalia of species of *Jardinella*. A-C, *J. isolata*, Stn 21(C), A, penis, B,C, oviduct; D–F, *J. eulo*, Stn 11, D, penis, E,F, oviduct. The heavy black line represents the posterior wall of the pallial cavity. ag – albumen gland; b – bursa copulatrix; cg – capsule gland; co – coiled oviduct; l – penial lobe or homologous area; o – oviduct opening; p – penial papilla; rc – rectal depression; sr – seminal receptacle; v – ventral channel or vestibule; vd – pallial vas deferens. Scales:- 0.25 mm.

*Dimensions:* see Table 3.

*Dimensions of holotype:* length 2.55 mm, width 2.64 mm, length of aperture 1.55 mm, number of teleoconch whorls 2.75.

*Operculum* (Fig. 32A): thin, light brown, 1.13-1.61 mm in length [mean 1.29 (M), 1.46 (F)]. With or without white smear up to 0.45 mm in length [mean 0.27 (M), 0.26 (F)]. Ratio of opercular length to position of nucleus 2.73-3.26 [mean 3.02 (M), 3.11 (F)].

*Dimensions:* see Table 3.

*Radula* (Fig. 32B): each central tooth with 3 lateral cusps; ratio of length of central cusp/length of adjacent cusp 1.7-1.9; 2 pairs of basal denticles; dorsal edge concave; basal process narrow, U-shaped, or basal process long, tongue shaped. Each lateral tooth with cusp formula (2-3).1.(2-3); ratio of length of primary cusp/length of adjacent outer cusps 1.7-1.8; with small basal bulge; outer shaft 2.4-2.6 times longer than cutting edge.

*Head-foot:* cephalic tentacles oval to circular in section, with no dorsal ciliated bands present; 2 distinct ciliated bands along most of ventral surface. Snout black on tops of concentric ridges, unpigmented between these ridges; distal end of snout unpigmented; dorsal sides of cephalic tentacles grey with unpigmented patch anterior to eyes; head and neck dark grey to black; sides of foot and opercular lobes pale grey. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity:* ctenidium with 24-25 filaments; apex on right. Osphradium between posterior end and middle of ctenidium. Hypobranchial gland very reduced or absent. No glandular pad to left of ctenidium, or near anus. Rectum with slight arch, anus with intermediate position relative to mantle edge. Kidney extends forward slightly into pallial roof.

*Male reproductive system* (Figs 33C,D, 34D): penial lobes distal; distal portion wrinkled, with short papilla at tip; middle part of penis with about 3 pale grey longitudinal stripes or unpigmented. Vas deferens straight or undulating.

*Female reproductive system* (Fig. 34E,F): pallial oviduct with unmodified ventral channel. Seminal receptacle lies opposite middle of bursa. Bursal duct arises from anterodorsal side of elongate bursa copulatrix which lies posterior to, and is larger than, albumen gland. Coiled oviduct and bursal duct fused to form common duct just in front of seminal receptacle duct. Coiled oviduct with proximal U-shaped loop and long posterior loop reaching almost to posterior edge of bursa copulatrix. Rudimentary penis absent in females.

**Remarks.** This species resembles *J. exigua* n.sp. in shape but is much larger and, unlike that species, possesses a bursa copulatrix. It differs from all other species of *Jardinella* in genital characters, having a penis bearing a club-shaped head and, like only *J. isolata* n.sp., has a non-coiled pallial vas deferens. The female system differs from all other species in the genus in having the coiled oviduct extending posteriorly almost to the posterior end of the bursa copulatrix after making a large loop in its proximal part.

Discriminate analysis shows that this species is most similar to *J. coreena* n.sp. and *J. edgbastonensis* n.sp. (Tables 5,6, Figs 35–37) in shell characters. It does, however, have a relatively broader spire than both of these species.

This species is known to live in two small springs near Eulo in southern Queensland. One potentially suitable habitat (Stn 10) close to Stn 11 had been dug out to form a large pond and no snails were present.

**Etymology.** The species is named for the town of Eulo in south-western Queensland.

## Phenetic Analysis

The discriminate analysis clearly indicates that all species are well distinguished on shell characters. Only two discriminate at less than 100% (18% of *J. edgbastonensis* are classified as *J. coreena* and 5% of *J. eulo* are classified as *J. carnarvonensis*). The generalised distances (given in Table 5) are discriminate space distances among centroids expressed in standard deviation units, the larger the number, the greater the difference between the groups. The Euclidean (or taxonomic) (see Table 6) distances assess the between centroid differences in reference to original variable coordinate axes. Plots of each population on the first three coordinates are given in Figs 35-37. Table 7 gives the percentage of the variance of each variable in each canonical variate to indicate the relative participation of each variable in each axis.

## Phylogenetic Analysis

A phylogenetic analysis was carried out to attempt to ascertain whether *Jardinella* was a monophyletic group and to try to obtain a picture of the evolution of the species within the genus. The data used in the phylogenetic analysis is given in Table 8. With one exception, all shell characters were omitted from the analysis as were all but two radular characters. Most shell and radular characters were omitted because they are mostly continuous (rather than discrete) and subject to homoplasy. Anatomical characters listed in Table 1 and not used in the phylogenetic analysis (i.e. not listed in Table 2) were either more-or-less uniform throughout all the taxa in the analysis, continuous (rather than discrete) characters, or considered to be of low value in determining relationships because of their plasticity and/or considerable homoplasy.

All of the taxa included in the analysis are part of what appears to be a monophyletic Australasian group of hydrobiids that share several characters. These include a non-glandular penis, non-pigmented coiled oviduct, a white layer on the inner side of the operculum

and two or more pairs of basal cusps on each central tooth of the radula. The subfamily name Tateinae is available for this group, but because higher category relationships in the hydrobiids are in need of major revision, we refer to this group as the *Tatea* group for the purposes of this paper.

We included *Jardinella thaanumi*, the type species of *Jardinella*, in the analysis although it falls well outside the spring radiation.

The outgroup chosen for this analysis is the estuarine genus *Tatea* which is judged to be the most plesiomorphic of all the Australian *Tatea* group. It has a protoconch of about two whorls with a distinctly separated protoconch 1 and protoconch 2. This latter character is assumed to be plesiomorphic and suggests a planktotrophic larval stage. It is the only genus in the *Tatea* group (including non Australian genera) to have this character. The remainder of the taxa in the analysis are assumed to be direct developers with a simple protoconch of about one and a half-whorls. Species of *Tatea*, *Fluvidona* and *Fonscochlea* typically have an operculum bearing pegs on its inner side, a character that is judged to be plesiomorphic for Australian Tateinae. A white smear, such as that seen in species of *Potamopyrgus* and *Fluviopupa*, may be more primitive but, in the case of these genera could equally well be secondarily reduced from an originally pegged condition.

The radula of species of *Tatea* and *Fluvidona* has three or more pairs of basal cusps on each central tooth, a character state plesiomorphic for the *Tatea* group. The outer shaft of each lateral tooth is more than 1.5 times as long as the length of the cutting edge in *Tatea* and most other genera of hydrobiids and this is taken to be the plesiomorphic state.

The pallial cavity is rather uniform throughout the

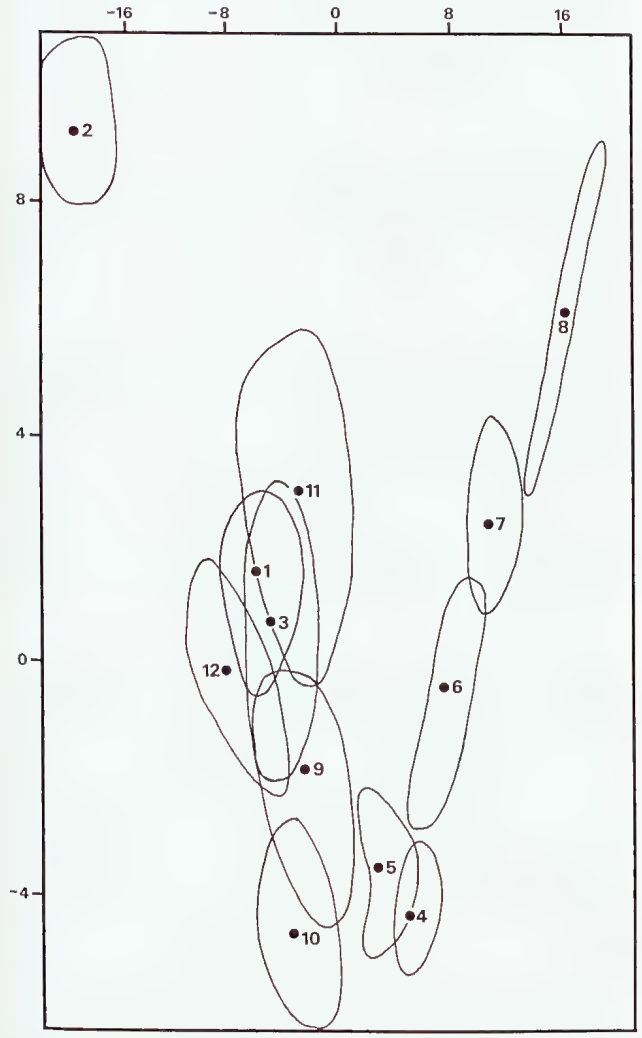


**Fig.35.** Plot of the results of the discriminate analysis using the first (vertical) and second coordinates. The group (species) centroids are indicated by a solid circle and a species number. The ellipses enclose all individuals of the species. 1 – *J. edgbastonensis*; 2 – *J. corrugata*; 3 – *J. coreena*; 4 – *J. pallida*; 5 – *J. colmani*; 6 – *J. jesswiseae*; 7 – *J. zeidlerorum*; 8 – *J. acuminata*; 9 – *J. carnarvonensis*; 10 – *J. exigua*; 11 – *J. isolata*; 12 – *J. eulo*.

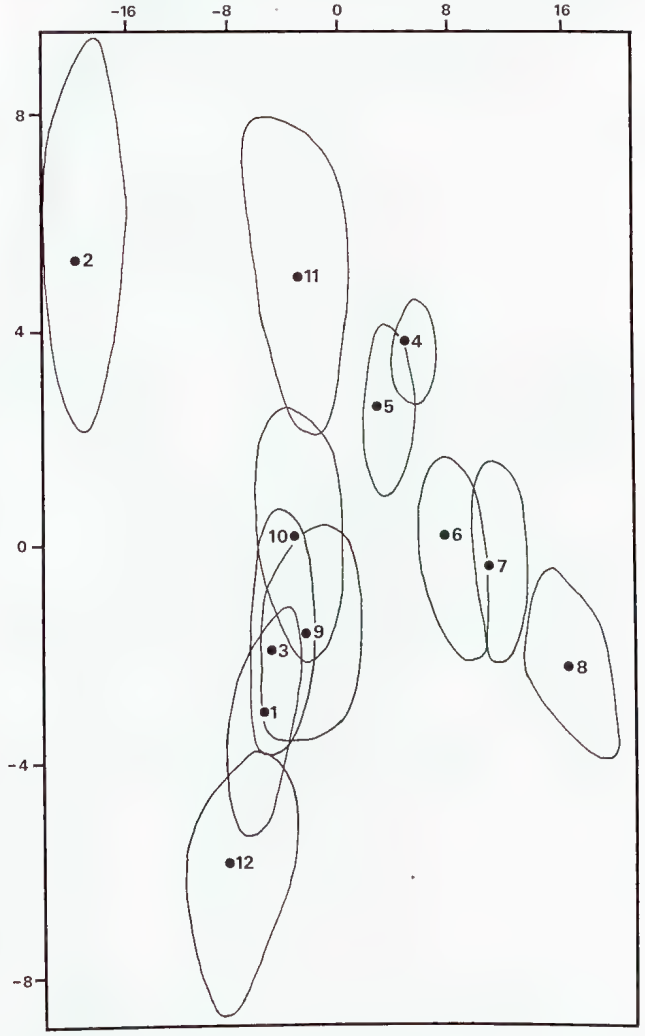


**Fig.36.** Plot of the results of the discriminate analysis using the first (vertical) and third coordinates. The group (species) centroids are indicated by a solid circle and a species number. The ellipses enclose all individuals of the species. 1 – *J. edgbastonensis*; 2 – *J. corrugata*; 3 – *J. coreena*; 4 – *J. pallida*; 5 – *J. colmani*; 6 – *J. jesswiseae*; 7 – *J. zeidlerorum*; 8 – *J. acuminata*; 9 – *J. carnarvonensis*; 10 – *J. exigua*; 11 – *J. isolata*; 12 – *J. eulo*.

group although the position of the osphradium relative to the posterior end of the gill varies from group to group. In *Tatea* and in *Hydrobia* it is located near the middle of the ctenidium and, consequently, this position is considered to be the plesiomorphic one. The presence of a hypobranchial gland is considered to be plesiomorphic as this structure is found in most neotaenioglossans. There is no glandular pad to the left of the ctenidium in species of *Tatea* or any other genus that we have examined, other than in two species of *Jardinella.*

The male genital system in species of *Tatea*, and in most other members of the *Tatea* group, is characterised by a simple, tapering penis, the distal end of which is wrinkled (in preserved material), a prostate gland that lies about half in and half behind the pallial roof and a more or less straight pallial vas deferens. The female system has a nonpigmented, U-shaped coiled oviduct with the small, ovoid seminal receptacle opening to it.

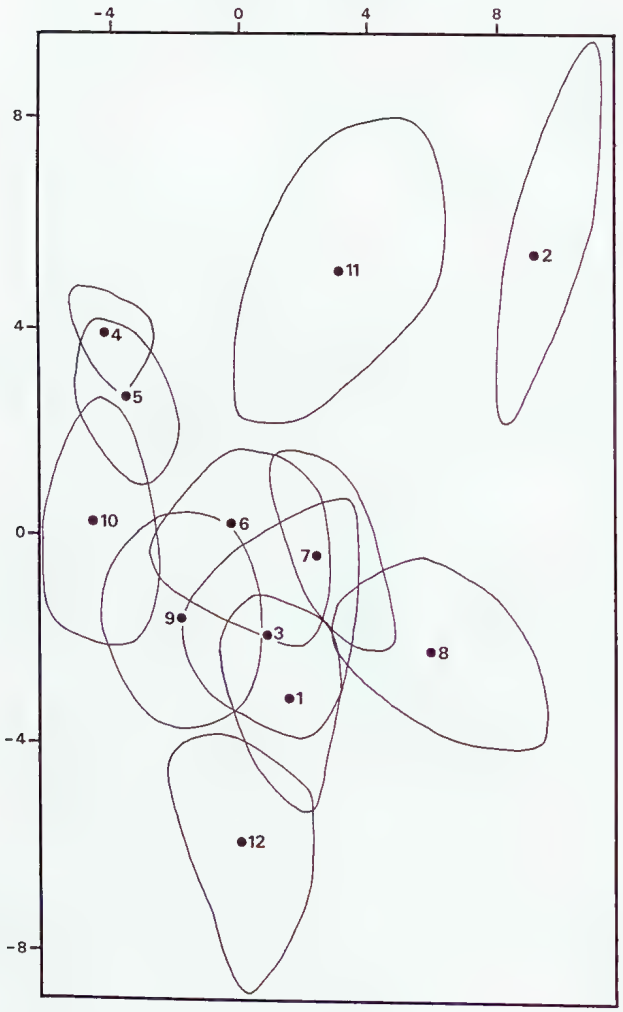


**Fig.37.** Plot of the results of the discriminate analysis using the second (vertical) and third coordinates. The group (species) centroids are indicated by a solid circle and a species number. The ellipses enclose all individuals of the species. 1 – *J. edgbastonensis*; 2 – *J. corrugata*; 3 – *J. coreena*; 4 – *J. pallida*; 5 – *J. colmani*; 6 – *J. jesswiseae*; 7 – *J. zeidlerorum*; 8 – *J. acuminata*; 9 – *J. carnarvonensis*; 10 – *J. exigua*; 11 – *J. isolata*; 12 – *J. eulo.*

The large bursa copulatrix lies behind the albumen gland, its duct running anteriorly from the anteroventral side of the bursa to join with the oviduct at the posterior wall of the pallial cavity. The oviduct opens to the ventral channel of the capsule gland which opens anteriorly by a simple, small opening. There is no rudimentary penis developed. All of these characters are taken to be plesiomorphic for the *Tatea* group for the purposes of this analysis.

Characters based on the patterns of ciliation of the cephalic tentacles are included in the analysis but we make no *a priori* assumptions about their polarity because of insufficient data about many of the other genera. The cephalic tentacles are oval in section in the majority of genera and this state is considered to be the plesiomorphous one.

The data was run (using PAUP) and 39 equally parsimonious trees (length = 55, consistency index = 0.60) were produced (Fig.38). *Tatea* was used as the outgroup to produce the consensus tree illustrated but using *Tatea* + *Fluvidona* or *Tatea* + *Fluvidona* + *Fonscochlea* as outgroups produced trees that were identical for the *Jardinella* clade and of the same length.

The ingroup is separated from the outgroup (*Tatea*) by two apomorphies, a reduced number of protoconch whorls, and the osphradium moving slightly posteriorly. *Fluvidona* is distinguished, in this analysis, by only one apomorphy — three ventral bands of cilia on the cephalic tentacles.

The clade formed by *Fonscochlea* and *Jardinella* is supported by three apomorphies, the only significant one being a reduction in the pairs of basal cusps on each central tooth of the radula to two (character 3B). The other two characters (dorsal ciliation of the cephalic tentacles and hypobranchial gland) are subject to reversals in the rest of the tree. The *Jardinella* clade is supported by three apomorphies:- the loss of opercular pegs and two related penial characters (the development of penial lobes and a smooth distal end).

Although this cladogram supports the monophyly of *Jardinella*, it also demonstrates the distinctiveness of *J. isolata* and *J. eulo.* This latter group is characterised by a unique apomorphy, an extra bend proximal to the U-shaped coiled oviduct (character 17C). It is also plesiomorphic in having the cephalic tentacles rounded in section (character 5A, of questionable value) and an uncoiled pallial vas deferens (character 13A). The branch leading to the remainder of the species of *Jardinella* is distinguished by the cephalic tentacles changing from oval to triangular in section (character 5B) and the acquisition of a coiled pallial vas deferens (character 13B).

The main cluster of species is not well resolved in the consensus tree and the following brief discussion outlines the main patterns observed. The characters given as distinguishing clades are the character state changes which occur at the stem of those groups. Several of these are, of course, subject to other state changes or reversals within the groups. Within this cluster *J. thaanumi* and *J. jesswiseae* form a polycotomy with the roots of three monophyletic groups which are present in all of

the trees. *Jardinella edgbastonensis*, *J. corrugata*, *J. coreena* and *J. pallida* + *J. colmani* form the largest of these monophyletic groups, which is distinguished by the pallial oviduct developing a papilla (character 20B). Within this clade, *J. pallida* and *J. colmani*, which are similar in shell characters, are defined in all trees as a monophyletic group in which the penis has reduced lobes and a long papilla (character 11D), the oviduct opening moves a little posteriorly (character 20C), and the oviduct and bursal duct join behind the posterior pallial wall (character 16B). This latter character is developed as a apomorphy of another pair of species having similar shell characters, *J. zeidlerorum* and *J. acuminata*, which are also characterised by anterior glandular pads in the pallial cavity (character 10B). The remaining pair of species, *J. carnarvonensis* and *J. exigua*, are distinguished by females having a rudimentary penis (character 21B) and a slit-like genital opening (character 19B).

Examination of the individual trees shows that the species in the eastern spring radiation (plus *J. thaanumi* ) fall into three groups. In one group (16 trees) two clades are formed - one with *J. jesswiseae*, *J. carnarvonensis* and *J. exigua* separated by two ventral bands of cilia on the tentacles (character 7B) and, in about half of these trees, a modified ventral channel (character 14B). The remainder of the species fall into the other group, which is distinguished by only one apomorphy, a long penial papilla (character 11D). This latter character change was the only one separating a group consisting of *J. thaanumi*, *J. zeidlerorum* and *J. acuminata* in ten trees, although in three additional trees this same group was distinguished by an additional character, a reversal of the development of the hypobranchial gland. In these 13 trees the remainder of the species are distinguished by two characters in eight trees, modification of the ventral channel and two ventral cilial tracts of the tentacles,

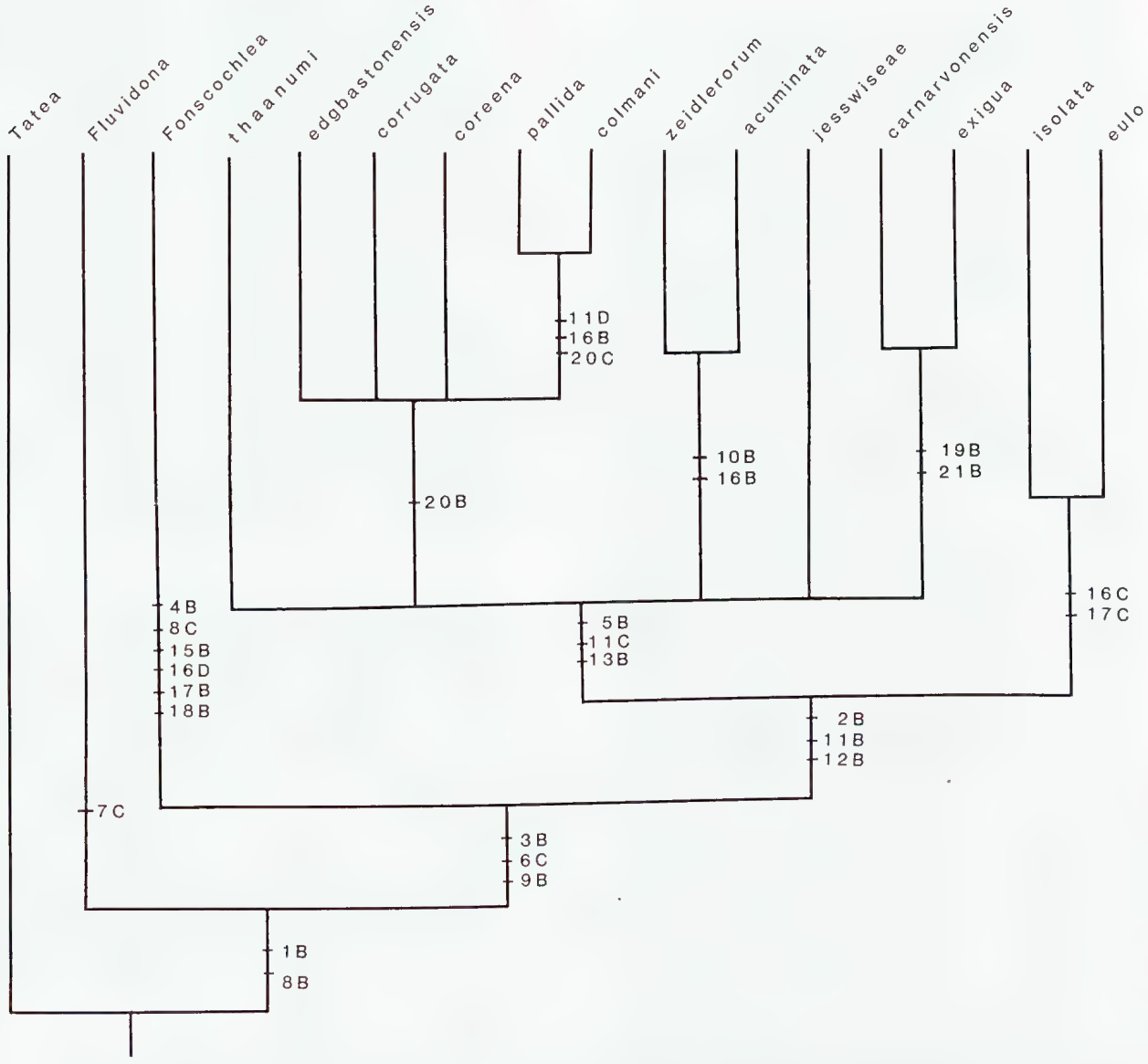


**Fig.38.** Strict consensus tree produced from 39 trees generated from the data given in Table 8. The numbers and letters along branches forming clades supported in all trees indicate character state changes. The branch lengths in no way reflect relative phylogenetic distance.

whereas in the other five trees either one of these two characters is utilised. The third pattern, seen in the remaining ten trees, *J. zeidlerorum* and *J. acuminata* separate as a separate group in the initial split which is distinguished by the characters given above (glandular pad + posterior joining of the oviduct and bursal duct). The stem giving rise to the remaining species shows no character changes.

Further resolution of species-level relationsips probably requires utilising additional characters, or character weighting, the latter not having been attempted with this data set. The analysis does, however, support the monophyly of *Jardinella*, its relationship to *Fonscochlea* and the basic division of the genus into western and eastern groups of species.

## Discussion

**Relationships with other genera.** *Jardinella* belongs to a group of mainly Australasian genera including *Tatea*, *Potamopyrgus* and *Fluvidona* which are similar anatomically and several of them possess the unusual feature (in the Hydrobiidae) of white material on the inner side of the operculum forming a smear or raised into one or more pegs. In mainland Australia, *Fluvidona* (*sensu lato*) is the only significant representative of this group of genera in freshwater and species referable to this genus extend around the coastal areas and along the Great Dividing Range from southern Queensland southwards to western South Australia and north into the Flinders Ranges as well as in south Western Australia (Ponder, unpublished). The only related genera, apart from the estuarine genus *Tatea*, are those found in Artesian springs associated with the Great Artesian Basin in South Australia [*Fonscochlea* (Ponder *et al.*, 1989) and a new genus from Dalhousie Springs (Ponder, 1989)] and Queensland (*Jardinella*). Although there is as yet insufficient data to demonstrate the detailed evolutionary relationships of these groups, we suggest that the cladogram shown in Fig. 38 indicates that the inland species evolved from a *Fluvidona*-like ancestor and that the artesian springs fauna may share a common ancestry.

The Queensland radiation (of *Jardinella*) is so diverse in shell and anatomical characters that this fauna must have been in existence for a considerable period of time. The Pleistocene radiation at Dalhousie Springs, while showing some divergence in shell shape and size and some physiological divergence (Ponder, 1989) has hardly differentiated anatomically (Ponder, unpublished observations). The radiation of *Fonscochlea* in the Lake Eyre Supergroup is diverse in shell characters but anatomically much more conservative (Ponder *et al.*, 1989) than seen in the *Jardinella* radiation. The sympatric *Trochidrobia* are, however, anatomically differentiated (Ponder *et al.*, 1989) but the relationships of this genus remain obscure. The Lake Eyre Supergroup hydrobiid fauna is presumably older than that at Dalhousie Springs as it was already well differentiated in the Pleistocene (from observations on fossils in Pleistocene mounds; Ponder, unpublished) and Miocene fossils from the general vicinity are similar to some *Fonscochlea* species (Ponder *et al.*, 1989). A mid-Tertiary origin of the Queensland artesian spring hydrobiid fauna is supported by the existence of Miocene limestones containing hydrobiids south-east of Springvale Homestead, north west of the Diamantina River in western Queensland (McMichael, 1968), about 46 km south-east of Elizabeth Springs where *J. isolata* is found living today. Thus both the Lake Eyre Supergroup hydrobiids and *Jardinella* may have had a common ancestor in the Miocene or even earlier.

The existence of two species (*J. exigua* and *J. carnarvonensis*) in springs not emanating from the Great Artesian Basin, but closely associated with the recharge areas on the eastern edge of the Basin (Springsure Supergroup), suggests that more similar species may be found in the extensive hinterland along the Great Dividing Range in this section of Queensland. The cladistic analysis clearly shows that these species are derived from the artesian spring radiation. Similarly *J. thaanumi*, the type species of *Jardinella*, lives in coastal streams and rivers in north Queensland (Ponder, in press B) and is clearly part of the same radiation.

The genus occurs in only four of the six supergroups of artesian springs recognised in Queensland (Habermehl, 1982; Ponder, 1986; see also Fig. 1) and currently there is no evidence to suggest that they once occurred in the other groups. It is, however, possible that further work may reveal living or extinct populations in those areas. The springs emanating from Tertiary basalts in the middle of the Great Artesian Basin and on the north eastern edge near Hughenden (Habermehl, 1982; see also Fig. 1D,H) lack hydrobiids of any sort. The only hydrobiid found in the other springs sampled was *Fluvidona* (*Posticobia*) cf. *brazieri* (Smith, 1882) from Stn 82 in a non-artesian spring in the Great Dividing Range west of Bundaberg. *Fluvidona* (*Posticobia*) *brazieri* is widely distributed in coastal rivers in northern New South Wales and southern Queensland.

**The radiation.** The species included in *Jardinella* consist of two main groups - the south-western group and the eastern group which probably diverged very early in the history of the genus. The south-western group (*J. eulo* and *J. isolata*) uniquely (within the genus) share some characters, some plesiomorphic (no coils in pallial vas deferens) and some derived (distal penial lobes) but also differ markedly from one another in other features (e.g. shell shape, posterior female genital characters) suggesting a long separation. These two species may be the surviving end points of what may have been a much larger radiation in this area. The eastern group of species is located in the Barcaldine and Springsure Supergroups on the eastern side of the Great Artesian Basin and, because more species still exist, it is possible to speculate on the evolution of this group.

The most derived members of this group may be the two species *J. acuminata* and *J. zeidlerorum*. These species possess a thick hypobranchial gland and autapomorphic glandular pads near the anus and on the left side of the ctenidium. The most similar species in shell characters,

*J. jesswiseae*, has the ventral channel modified as a vestibule, a character that is regarded as an autapomorphy of the eastern species of the genus (the exceptions are interpreted as reversals). Females of *J. jesswiseae* occasionally have a rudimentary penis and this feature is characteristic of the two species found in non-artesian springs (*J. carnarvonensis* and *J. exigua*). These latter two species have short-spired shells, a character shared with several species living in the artesian springs. *Jardinella coreena* and *J. corrugata* appear to be related, sharing rather similar reproductive characters, especially the penial lobes. *Jardinella edgbastonensis* also has a similar shell, but a different penis, although it would be possible to derive the penis of that species from one like that in *J. coreena* and *J. corrugata* by reduction of the penial folds. Presumably *J. thaanumi* was derived from a species somewhat similar to *J. edgbastonensis* that evolved on the western side of the Great Dividing Range rather than the artesian spring radiation being derived from the east because the more primitive members of the *Jardinella* clade are present in western-most Queensland.

Two allopatric species sharing similar shells and genital characters are *J. colmani* and *J. pallida* which are intermediate in shell shape between species such as *J. jesswiseae* and *J. edgbastonensis*.

All of the springs containing hydrobiids have a single

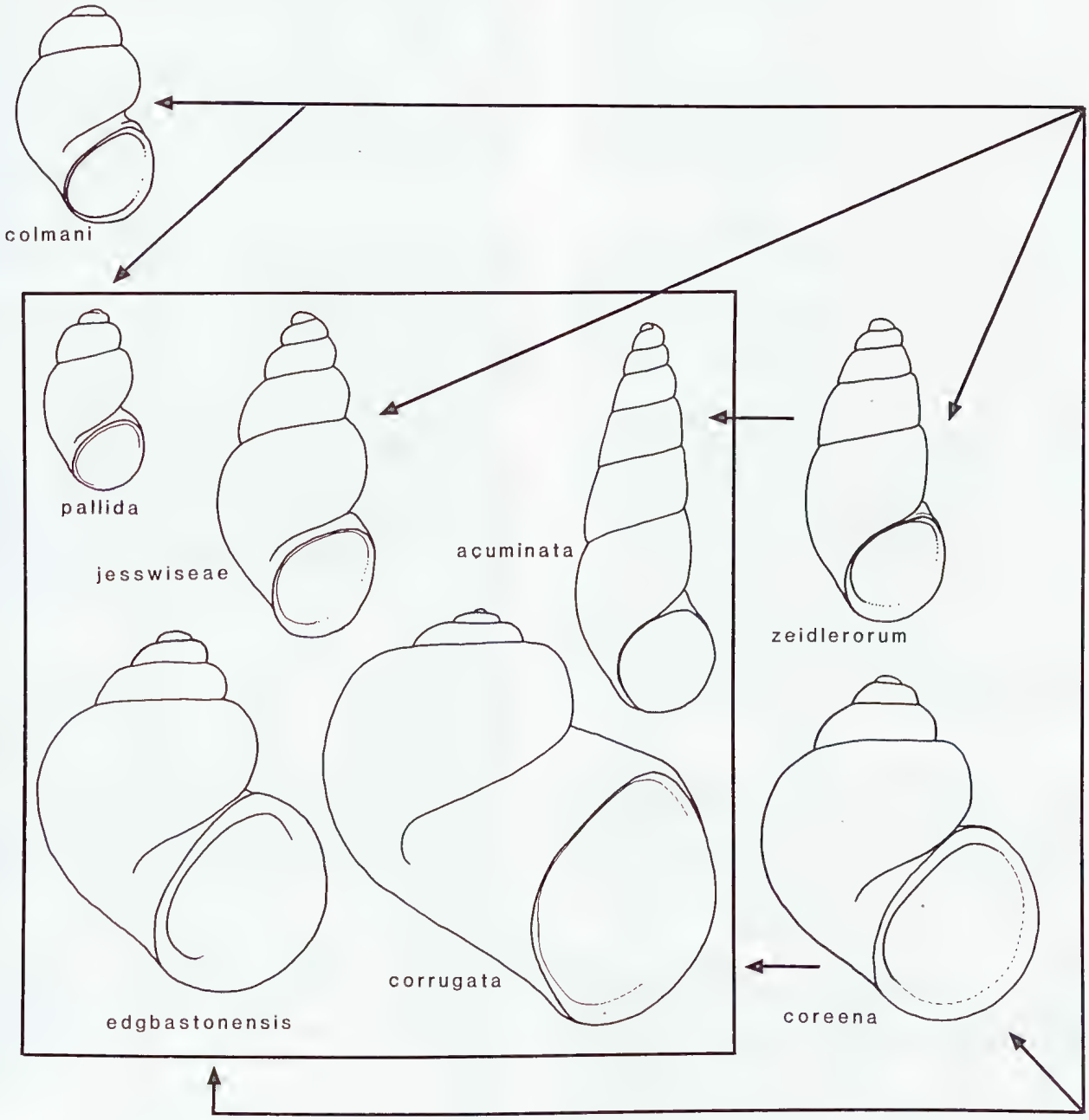


**Fig.39.** A diagrammatic representation of the possible origin of the hydrobiid fauna of Edgbaston springs. The species enclosed in the square are those living sympatrically at Edgbaston Springs, those outside the square live in the general vicinity. The lines represent probable relationships, the arrows the possible migration of an ancestral taxon in relation to Edgbaston Springs.

species except Edgbaston Springs. Of the five described species living in Edgbaston Springs (the sixth undescribed species cannot be included in this discussion because only the shell characters are known) there is some evidence to suggest that three of these evolved allopatrically and subsequently differentiated after dispersal events carried them to Edgbaston Springs (Fig. 39). *Jardinella pallida* is rather similar to *J. colmani* which occurs in springs about 58 km to the north. There are a number of springs in this area, some of which are recently extinct or heavily degraded and some of which have not been investigated. It is quite possible that *J. colmani* was (or is) more widespread or that other similar species are living in the general area. *Jardinella acuminata* is clearly closely allied to *J. zeidlerorum* which lives in a spring only about 11 km from Edgbaston Springs. These two species are not clearly related to any others. The Edgbaston species *J. corrugata* is similar, as noted above, to *J. coreena*, which lives 61 km to the south, and they may have shared a common ancestry but, again, there is no clear relationship with other species except perhaps *J. edgbastonensis*.

In these three cases allopatric evolution followed by dispersal to Edgbaston Springs appears to have occurred because it can be shown that existing species outside Edgbaston Springs are morphologically similar. The idea that these species have migrated to Edgbaston Springs (and not vice versa) is supported by most Edgbaston derivatives being more apomorphic.

The relationships of *J. jesswiseae* are more obscure. It may be an offshoot from the common ancestor to *J. colmani* + *J. pallida* and *J. acuminata* + *J. zeidlerorum*. Certainly the possession of a deviated protoconch allies it to the latter two species (this character was not included in the cladistic analysis).

Other species of molluscs at Edgbaston Springs included *Gabbia* sp. (Bithyniidae), a species somewhat similar in size and shape to *J. corrugata* and *J. edgbastonensis*. The families Ancylidae and Planorbidae represented by one (*Ferrissia* sp.) and two (*Gyralus* sp. and *Isidorella* sp.) species respectively.

**Evolution of major characters.** *Shell.* The acceptance of the remarkable diversity of shell form as part of a single radiation is perhaps made more acceptable because there is a gradation between all of the shell types. The uniformity of the group is also supported by the identical microsculpture of the protoconch in all species.

*Operculum.* The operculum differs from most related genera in lacking pegs on the inner surface (although sometimes there is a low horny swelling) but usually has a white smear. This latter character strongly suggests that the pegs were present in an ancestral form but have subsequently been lost. Likewise the white smear is lacking in some individuals of most species and in all individuals of some species.

*Radula.* The radular characters are similar to those of *Fonscochlea* in typically having only two pairs of basal cusps on the central teeth but those of *Jardinella* are more plesiomorphic because they have longer shafts on the lateral teeth in almost all species. Occasional specimens of *Jardinella* are found with a third pair of cusps (usually only on one side of the tooth) supporting the idea that the two-cusp condition is derived from a multi-cuspid state.

*Male genitalia.* A distinctive character of several of the species of *Jardinella* is the development of flattened, pigmented, non-glandular lobes on the penis. The ancestral condition of this state appears to have been the development of this structure in the medial part of the penis, with a smooth (i.e. essentially non-contractile), portion distal to it that tapers to a point where the penial duct opens. The relative development of the lobes and the length of the distal portion relative to the rest of the penis appear to explain the majority of variation in penial morphology in the group. Those species appearing to have a simple penis, resembling that of species of *Fluvidona*, differ from species in that group in having the distal part of the penis non-contractile (i.e. smooth when fixed in the resting position), not contractile (i.e. wrinkled when fixed in the resting position). For this reason it is assumed that these species have lost the lobes/swellings and resemble the simple, tapering penis of species of *Fluvidona* only superficially.

Another apomorphy of most species of the genus is the coiled pallial vas deferens, a character seen in all species except *J. isolata* and *J. eulo*. *Fonscochlea* species have a plesiomorphic penial morphology and pallial vas deferens resembling those of *Fluvidona*.

*Female genitalia.* In its plesiomorphic state the ventral channel is open to the capsule gland along its entire length. The most unusual feature of the pallial oviduct in some species of *Jardinella* is the formation of a muscular vestibule characterised by being partially separated from the capsule gland and with folded internal walls. This feature, however, is absent in both the western species and in three of the eastern species. The sperm channel is separated by a flap of ciliated tissue (the lateral fold) in the plesiomorphic state, this becoming separated as a wide duct lying on the inner (left) side of the capsule gland when defined as a vestibule. There may have been reversals to a plesiomorphic-like state in *J. acuminata*, *J. zeidlerorum* and *J. exigua*. Some evidence for a reversal in the latter species is that it appears to have been derived from an ancestor similar to *J. carnarvonensis* with a vestibule but has reverted to a state resembling the ancestral one, apart from sharing the long pallial opening.

A rudimentary penis is found consistently in females of *J. exigua* and *J. carnarvonensis* and in a few females of *J. jesswiseae*. The latter was scored as state A in the cladistic analysis because, given the small number of individuals examined for most species, occasional rudimentary penes could have been missed in other species. We have no explanation as to why rudimentary penes should occur. Certainly there is no evidence of protandry.

**Conservation considerations.** Of the species described in this paper, all but one is endangered. While

*J. carnarvonensis* is contained in a National Park, the habitat of none of the others is protected in any way, all being on pastoral land. Several species are in small springs that are easily damaged — for example *J. eulo* is known from only two springs, but a dam had been dug out of a third one (Stn 10) which was located close to one of the springs containing snails (Stn 11) and no snails were present. All species are found only in single springs or in small, tightly grouped springs.

There are several ways the habitats could be degraded causing the extinction of the molluscs and other aquatic fauna. These include:-

1. Direct damage by pastoralists – e.g. damming, digging out, placing a well on or near the spring, overstocking.

2. Indirect damage – general drawdown from artesian wells leading to reduced flow (with consequent reduction of habitat) and eventual cessation of flow.

Feral and pastoral stock damage caused by overstocking and inadequate control of feral animals (e.g. horses, camels, donkeys) is a problem but generally the springs should recover unless the damage is extreme.

Direct damage from pastoralists can be prevented by education or specifically protecting the spring areas. The problem of drawdown caused by the over-exploitation of artesian water is a far reaching one that needs to be addressed on an interstate level [see Habermehl (1980) for a general overview]. Many Queensland, and virtually all New South Wales artesian springs have become extinct since the 1880's (Habermehl, 1980, 1982; Ponder, 1986; see also Fig. 1). If the removal of artesian water is not adequately controlled the extinction of most of the remaining Queensland artesian springs is assured. Many of the springs recorded by Habermehl (1980) proved to be extinct when visited on the 1984 survey (Fig.1).

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## APPENDIX 1

### List of Stations

In the list of stations given below, the original field numbers are given. Distances from major locations (e.g. towns) are straight line distances taken from the map. Minor distances are generally distances by road measured with a vehicle speedometer. Map sheet names are the Queensland 1:250,000 series.

#### Springs Containing Hydrobiids

8, unnamed spring at Tunga Bore near Mount Tunga about 43 km west-south-west of Eulo, 28°13'S 144°38'E. Eulo 252 498. WFP and PHC, 6 Sept. 1984.

11, "Rocky Springs" near Mount Francis about 52 km south-west of Eulo, 28°18'S 144°32'E. Eulo 244 489. WFP and PHC, 7 Sept. 1984.

21, Elizabeth Springs about 26 km north-north-west of Springvale, 23°20'30"S 140°34'40"E. Springvale 457 418. WFP and PHC, 10 Sept. 1984. A – top of spring; B – outflow; C – large seep; D – small seeping pool on side of creek.

Z1, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Low mound nearest creek.

Z2, Elizabeth Springs, about 95 km south-east of Boulia, 23°20'30"S 140°34'40"E. Springvale 457 418. WZ, 23 Apr. 1988. Mound adjacent to spring with old fence about 300 m north of Stn Z1.

71, unnamed spring near Smokey Creek about 8 km east-north-east of "The Springs" HS, about 83 km north-north-east of Aramac, 22°12'20"S 145°22'30"E. Muttaburra 332 544. WFP and PHC, 25 Sept. 1984.

72, unnamed spring 2.3 km north-east of "Edgbaston" HS, about 34 km north-east of Aramac, 22°43'30"S 145°25'30"E. Muttaburra 338 486. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 220 m, on open plain. A – general; B – head of spring, in *Phragmites*; C – on sheep's skull; D – middle of outflow 50 m from head; E – edge of outflow 50 m from head; F – 20 m from end of outflow.

73, "Big Spring" about 3 km south-east of "Edgbaston" HS, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WFP and PHC, 26 Sept. 1984. Large spring with outflow about 170 m. A – upper outflow; B – lower part of outflow; C – small seep; D – head of spring.

74, unnamed spring about 3.6 km south-east of "Edgbaston" HS, about 30 km north-east of Aramac, 22°45'30"S 145°25'30"E. Muttaburra 339 483. WFP and PHC, 26 Sept. 1984. Small spring in low sandhills on the edge of a claypan.

Z6, unnamed spring about 11 km north-east of "The Springs" HS, about 83 km north of Aramac, 22°12'20"S 145°22'30"E. Muttaburra 332 544. WZ, 2 May 1988. Low mound (fenced) with ill-defined source and small outflow.

Z7, unnamed spring about 2.4 km north-east of "Edgbaston" HS, about 33 km north-east of Aramac, 22°42'45"S 145°25'25"E. Muttaburra 338 487. WZ, 3 May 1988. No mound but extensive seepage.

Z8, unnamed spring about 2.3 km north-east of "Edgbaston" HS, about 33 km north-east of Aramac, 22°43'S 145°25'30"E. Muttaburra 338 487. WZ, 3 May 1988. Low mound with outflow of about 60 m.

Z9, "Big Spring" about 3 km south-east of "Edgbaston" HS, about 31 km north-east of Aramac, 22°45'S 145°25'30"E. Muttaburra 337 483. WZ, 4 May 1988. Large spring. A – outflow; B – from flood plain.

Z10, unnamed spring about 3.3 km south-east of "Edgbaston" HS, about 31 km north-east of Aramac, 22°45'30"S 145°25'40"E. Muttaburra 339 483. WZ, 4 May 1988.

Z12, unnamed spring about 11 km south-south-east of "Edgbaston" HS, about 0.8 km south of main road, about 28 km north-east of Aramac, 22°47'20"S 145°25'40"E. Muttaburra 339 479. WZ, 4 May 1988. Mud mound supporting large natural pool.

Z14, large unnamed spring just south of "Coreena" HS, about 32 km north-east of Barcaldine, 23°17'S 145°24'E. Longreach 337 425. WZ, 5 May 1988.

82, Belinda Spring, Salvator Rosa Section, Carnarvon Gorge National Park, 24°50'S 147°11'45"E. Springsure 519 254. WFP and PHC, 29 Sept. 1984. Large spring with outflow about 120 m.

88, small unnamed spring on hillside about 2.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984.

89, small unnamed spring on hillside about 100 m south-east of Stn 88, about 2.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°47'E. Springsure 582 249. WFP and PHC, 30 Sept. 1984. Head of spring fenced off and a small pipe leading from it.

93, Small seep about 1.2 km north-east of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°48'E. Springsure 581 249. WFP and PHC, 1 Oct. 1984. With small pipe leading from it. A – head of spring; B – outflow.

Z15, unnamed spring about 5 km north-west of Rangers HQ, just north of 13th river crossing, Carnarvon Gorge National Park, 25°02'30"S 148°11'20"E. Eddystone 619 229. WZ, 8 May 1988.

Z16, small seep from rock face east side of Kooraminya

Creek, about 200 m up gorge, about 7.3 km west of Rangers HQ, Carnarvon Gorge National Park, 25°02'20"S 148°11'E. Eddystone 619 229. WZ, 8 May 1988.

Z17, unnamed side spring, about 300 m up Hellhole Gorge (Koolaro Creek), about 3 km west of Rangers HQ, Carnarvon Gorge National Park, 25°03'30"S 148°12'30"E. Eddystone 622 228. WZ, 8 May 1988.

### Springs Not Containing Hydrobiids

2, unnamed springs about 10 km east-north-east of Eulo, on tributary of Gumble Creek, 28°07'S 145°09'E. Eulo 307 513. WFP and PHC, 5 Sept. 1984. 15-20 small springs extinct to nearly extinct (damp mud).

3, unnamed springs about 2 km south-west of Eulo, 28°10'30"S 145°01'E. Eulo 294 506. WFP and PHC, 5 Sept. 1984. A few low extinct mounds.

4, unnamed springs about 10 km west of Eulo, on side of road, 28°08'45"S 144°57'E. Eulo 288 508. WFP and PHC, 5 Sept. 1984. Three large mounds all slightly damp.

5, mud spring about 20 km west of Eulo, Yowah Creek, on side of road, 28°07'30"S 144°51'30"E. Eulo 277 510. WFP and PHC, 5 Sept. 1984.

6, Dewalla "Spring" near bore about 34 km west of Eulo on Dewalla Creek, 28°07'50"S 144°43'30"E. Eulo 263 511. WFP and PHC, 5 Sept. 1984. One old low mound.

7, unnamed spring at "Bingara" HS about 38 km west of Eulo, 28°09'30"S 144°43'30"E. Eulo 263 507. WFP and PHC, 5 Sept. 1984.

9, Wombula Springs near Tunga Bore about 73 km west-south-west of Eulo, 28°16'20"S 144°19'20"E. Eulo 220 492. WFP and PHC, 6 Sept. 1984. About 10 mud mounds and several seepages.

10, Granite Springs near Mount Francis about 53 km south-west of Eulo, 28°19'S 144°32'E. Eulo 243 487. WFP and PHC, 6 Sept 1984. Large spring bulldozed to make deep pool for water supply.

12, unnamed springs 7 km south of "Granite Springs" HS, about 60 km south-west of Eulo, 28°23'45"S 144°30'30"E. Eulo 240 476. WFP and PHC, 7 Sept. 1984. Several extinct mound springs.

13, unnamed springs about 7.5 km north-west of "Currawinya" HS, about 90 km south-south-west of Eulo, 28°47'S 144°28'30"E. Eulo 231 431. WFP and PHC, 7 Sept. 1984. Large group of extinct mounds with a few damp ones on the eastern edge of group.

14, unnamed spring north of Fish Spring Bore about 89 km south-south-west of Eulo, 28°44'30"S 144°25'E. Eulo 231 435. WFP and PHC, 7 Sept. 1984. Two extinct mounds.

15, unnamed springs near Shire Council Tank about 85 km south-west of Eulo, 28°40'30"S 144°24'45"E. Eulo 231 441. WFP and PHC, 7 Sept. 1984. A few extinct mound springs.

16, unnamed spring (not artesian) in Touro Creek about 88 km south-east of Windorah, 25°57'30"S 143°17'30"E. Windorah 652 771. WFP and PHC, 8 Sept. 1984. Large pool and small runoff from a smaller pool, both with stagnant, oily water.

17, about 4-5 small non-artesian seeps and small pool in Touro Creek about 89 km south-east of Windorah, 25°58'30"S 143°17'30"E. Windorah 651 768. WFP and PHC, 8 Sept. 1984.

18, two pools (not artesian) in Touro Creek about 91 km south-east of Windorah, 25°57'30"S 143°19'30"E. Windorah 655 770. WFP and PHC, 8 Sept. 1984. One large and one small pool, the small probably spring fed.

19, unnamed spring (not artesian) about 23 km north-north-west of Windorah, 25°14'S 142°34'30"E. Windorah 575 863. WFP and PHC, 9 Sept. 1984. The spring has been dug out to form a well about a metre deep.

26, mud pan about 25 km north-north-west of Julia Creek, 20°26'S 141°40'E. Julia Creek 569 739. WFP and PHC, 13 Sept. 1984. Pan about 100 m wide with a few small mud "bubbles" just damp, no standing water.

27, spring remains about 2 km north-north-west of "Alva Downs" HS, about 28 km north-north-west of Julia Creek, 20°24'S 141°38'30E. Julia Creek 567 744. WFP and PHC, 13 Sept. 1984. A few low sand and clay mounds along spring bank.

28, unnamed spring about 6 km north of "Alva Downs" HS, about 35 km north-north-west of Julia Creek, 20°21'S 141°38'E. Julia Creek 567 744. WFP and PHC, 13 Sept. 1984.

29, unnamed spring on Spring Creek a tributary of Flinders River about 37 km north-west of "Numil" HS, 19°33'S 141°06'E. Millungera 412 551. WFP and PHC, 14 Sept. 1984. The spring has been made into a well, there are several other extinct springs in the area.

30, bore on Boorabin Creek about 0.5 km downstream from Malpas Bore, about 10 km east of "Malpas" HS, 19°35'S 142°19'20"E. Millungera 553 544. WFP and PHC, 15 Sept. 1984.

31, "Plain Spring" on tributary of Currajong Creek, about 6.5 km north-east of Stn 30, about 15 km east of "Malpas" HS, 19°33'30"S 142°21'30"E. Millungera 557 549. WFP and PHC, 15 Sept. 1984. A large low mound, spring extinct.

32, unnamed spring about 12 km north-north-east of "Malpas" HS, 19°30'30"S 142°17'30"E. Millungera 550 555. WFP and PHC, 15 Sept. 1984. Extinct spring.

33, pool just north of Stn 32, about 12.3 km north-north-east of "Malpas" HS, 19°30'30"S 142°18'E. Millungera 551 555. WFP and PHC, 15 Sept. 1984. Circular depression scrapped out and full of water.

34, large shallow muddy pool about 1.8 km north of Stn 32,

on east side of road, about 13.8 km north-north-east of "Malpas" HS, 19°30'S 142°17'45"E. Millungera 552 556. WFP and PHC, 15 Sept. 1984. Probably a spring.

35, "Black Spring" about 25 km north-east of "Malpas" HS, 19°29'S 142°25'E. Millungera 565 558. WFP and PHC, 15 Sept. 1984. Large mound spring.

36, unnamed spring about 20 km south-east of "Malpas" HS, 19°46'S 142°20'E. Millungera 554 525. WFP and PHC, 16 Sept. 1984. Extinct spring.

38, unnamed spring at "Saxby Downs" HS, 20°02'S 142°29'E. Julia Creek 655 784. WFP and PHC, 16 Sept. 1984. Spring with deposits of sulphur and iron, with no signs of life present in the spring.

39, Waddy Springs about 1.5 km south-east of "Saxby Downs" HS, 20°03'S 142°29'E. Julia Creek 657 783. WFP and PHC, 16 Sept. 1984. Small muddy pools with algae, badly polluted and damaged by cattle.

40, unnamed spring about 6 km east-south-east of "Saxby Downs" HS, 20°03'S 142°32'E. Richmond 661 783. WFP and PHC, 16 Sept. 1984. Small muddy spring in hollow, heavily polluted.

45, Peelunga Spring about 9.5 km north-west of Mount Whelan, 23°24'30"S 138°48'45"E. Mount Whelan 276 411. WFP and PHC, 18 Sept. 1984. An extinct travertine spring.

46, Peanunga Spring about 8.5 km west of Mount Whelan, 23°26'S 138°48'30"E. Mount Whelan 275 407. WFP and PHC, 18 Sept. 1984. A large low seeping mound spring.

47, New Carlo Spring about 6.5 km west of Mount Whelan, 23°26'30"S 138°49'30"E. Mount Whelan 277 406. WFP and PHC, 18 Sept. 1984. A mound of carbonate with large hole in one side containing water, and a pool with mud spring feeding it about 60 m away, heavily polluted by cattle.

48, Kendalls Spring about 8.5 km west-south-west of Mount Whelan, 23°28'S 138°49'E. Mount Whelan 276 403. WFP and PHC, 18 Sept. 1984. Small mud spring with shallow muddy pool.

49, unnamed springs about 12.5 km south-south-west of Mount Whelan, 23°30'30"S 138°47'30"E. Mount Whelan 274 398. WFP and PHC, 19 Sept. 1984. Several damp sand mounds on a large flood plain.

50, unnamed spring about 14 km south-south-west of Mount Whelan, 23°31'S 138°47'E. Mount Whelan 273 398. WFP and PHC, 19 Sept. 1984. A low, flowing spring on a large flood plain.

51, unnamed spring about 0.5 km east of Stn 49, about 13 km south-south-west of Mount Whelan, 23°31'S 138°48'E. Mount Whelan 274 399. WFP and PHC, 19 Sept. 1984. Cattle trampled spring.

52, Allawonga Springs about 27 km south-west of Mount Whelan, 23°33'30"S 138°40'E. Mount Whelan 262 392. WFP and PHC, 19 Sept. 1984. A low mound spring, with some cattle damage.

53, Allawonga Springs about 27 km south-west of Mount Whelan, 23°33'30"S 138°40'30"E. Mount Whelan 263 392. WFP and PHC, 19 Sept. 1984. Two small springs about 6 m apart.

54, Mulligan River, about 29 km south-south-west of Mount Whelan, 23°40'S 138°45'E. Mount Whelan 272 381. WFP and PHC, 19 Sept. 1984. Several still, clear connected pools.

55, unnamed springs on north-west side of Mulligan River about 1 km south-west of Stn 54, about 30 km south-south-west of Mount Whelan, 23°40'30"S 138°45'E. Mount Whelan 271 381. Several small low oozing mud springs. WFP and PHC, 19 Sept. 1984.

56, Wongitta Waterhole about 44 km south-west of Mount Whelan, 23°45'S 138°38'30"E. Mount Whelan 259 371. WFP and PHC, 19 Sept. 1984. Long, shallow pool.

57, Pitchamurra Spring about 46.5 km south-south-west of Mount Whelan, 23°47'S 138°39'30"E. Mount Whelan 261 367. WFP and PHC, 20 Sept. 1984. Very polluted spring, cattle trodden.

58, Mirrica Springs about 61.5 km south-west of Mount Whelan, 23°51'30"S 138°30'E. Mount Whelan 246 369. WFP and PHC, 20 Sept. 1984. Tiny pools of water in creek.

62, unnamed springs near Datson Bore, about 54 km east of Boulia, 22°51'S 140°24'30"E. Boulia 336 151. WFP and PHC, 21 Sept. 1984. Line of small springs and seeps along a creek bed.

63, Pathungra Spring about 5 km south-west of "Pathungra" HS, about 83 km north-east of Boulia, 22°24'30"S 139°35'E. Boulia 352 205. WFP and PHC, 21 Sept. 1984. Old bore on what was a spring.

66, Soda Gorge Spring about 27.5 km north-west of Hughenden, 20°37'S 144°05'30"E. Hughenden 197 717. WFP and PHC, 23 Sept. 1984.

69, Mickey Spring on tributary of Flinders River, about 67 km north-east of Hughenden, 20°23'S 144°37'30"E. Hughenden 252 743. WFP and PHC, 24 Sept. 1984.

70, downstream of Mickey Spring, about 65 km north-east of Hughenden, 20°24'30"S 144°37'E. Hughenden 251 742. WFP and PHC, 24 Sept. 1984. Small seeping spring.

75, unnamed spring at "Texas" HS, about 64 km north-west of Jericho, 23°05'S 145°50'30"E. Jericho 382 447. WFP and PHC, 26 Sept. 1984. Large spring with calcrete rock in abundance but dug out and covered at head.

76, Four Mile Spring about 59 km north-west of Jericho, 23°08'S 145°50'E. Jericho 381 441. WFP and PHC, 26 Sept. 1984. Spring with a pumping mill associated with it.

77, small unnamed spring about 200 m south of Ten Mile Spring, about 51 km north-west of Jericho, 23°12'30"S 145°51'E. Jericho 382 433. WFP and PHC, 26 Sept. 1984.

78, small unnamed seepage/spring about 1 km north of "Igtham" HS, about 21 km west of Jericho, 23°34'S 145°54'30"E. Jericho 389 394. WFP and PHC, 27 Sept. 1984. Small flow, with heavy cattle pressure.

81, small unnamed spring about 51 km north-west of Tambo, 24°27'45"S 146°03'30"E. Tambo 403 294. WFP and PHC, 28 Sept. 1984. Two small springs one with piping feeding from it, with cattle degradation extensive for both springs.

83, Major Mitchell Springs, Salvator Rosa Section, Carnarvon Gorge National Park, 24°51'40"S 147°11'E. Springsure 519 251. WFP and PHC, 29 Sept. 1984. Large valley with swampy springs on floor.

84, peat bogs about 2.5 km north of Major Mitchell Springs and about 1.5 km south of Belinda Spring, Salvator Rosa Section, Carnarvon Gorge National Park, 24°50'30"S 147°11'30"E. Springsure 519 252. WFP and PHC, 29 Sept. 1984. Large swampy gullies with swift narrow channels and numerous seeps.

85, small unnamed bog/spring on side of track on tributary of Nogoa River, about 5.2 km north along track from Belinda Spring, Salvator Rosa Section, Carnarvon Gorge National Park, 24°48'30"S 147°11'E. Springsure 518 256. WFP and PHC, 29 Sept. 1984.

86, large unnamed spring, in Reedy Creek at "Crystalbrook" HS, south of Carnarvon Gorge National Park, 25°30'30"S 147°58'30"E. Eddystone 598 179. WFP and PHC, 30 Sept. 1984. Cattle damage throughout spring but not very bad.

90, small seep/spring in narrow gully, about 1 km north of Stn 88, about 3.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°51'S 147°47'E. Springsure 579 250. WFP and PHC, 1 Oct. 1984.

91, small seep/spring in narrow gully, about 1 km south-west of Stn 88, about 2.5 km north-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°52'S 147°46'E. Springsure 578 248. WFP and PHC, 1 Oct. 1984.

92, small seep, in large creek gully, about 1.5 km north-east of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°51'30"S 147°48'20"E. Springsure 582 248. WFP and PHC, 1 Oct. 1984.

94, "Black Bull Spring" about 11 km north-east of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°47'S 147°51'E. Springsure 587 258. WFP and PHC, 1 Oct. 1984. Large spring.

95, unnamed spring about 13 km north of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°46'S 147°49'E. Springsure 583 259. WFP and PHC, 1 Oct. 1984. Similar to last spring but smaller.

96, Paddys Spring about 8 km south-west of "Dooloogarah" HS, south of Carnarvon Gorge National Park, 24°56'S 147°50'45"E. Springsure 585 242. WFP and PHC, 1 Oct. 1984. Large waterhole in narrow sandstone gully/gorge.

97, unnamed spring about 1.5 km north of "Mount Hutton" HS, about 21.5 km east of Injune, 25°49'50"S 148°46'40"E. Taroom 678 143. WFP and PHC, 2 Oct. 1984. Large swampy spring in depression near Injune Creek.

98, unnamed springs about 1.5 km north of Stn 97, about 21 km east of Injune, 25°48'S 148°46'E. Taroom 678 146. WFP and PHC, 2 Oct. 1984.

## APPENDIX 2

Table 1. List of characters and character states used in compiling the descriptions. Those also used in the phylogenetic analysis are indicated by an asterisk (*).

### Shell

Shell shape
1. trochiform (length/width ratio 0.50-1.30)
2. conical (length/width ratio 1.30-2.01)
3. elongate conic (length/width ratio 2.01-2.30)
4. very elongate conic (length/width ratio 2.30-2.80)

Shell size
1. small (length 1.0-2.0 mm)
2. of medium size (length 2.0-3.6 mm)
3. large (length greater than 3.6 mm)

Shell length and width
Shell thickness (not quantified)
Shell colour (observed dry)
Periostracum - including colour
Spire angle
* Number of protoconch whorls
Protoconch microsculpture
Number of teleoconch whorls
Convexity ratio
Teleoconch sculpture
Slope of growth lines on teleoconch
Shape of periphery of body whorl
Aperture length/shell length ratio
Thickening of inner lip
Width of inner lip
Columellar swelling present or absent
Slope and angle of outer lip
Umbilicus
1. closed
2. minute (width of body whorl/width of umbilicus greater than 26)
3. small (width of body whorl/width of umbilicus 10-26)
4. medium (width of body whorl/width of umbilicus 4-10)
5. wide (width of body whorl/width of umbilicus 1-4)

Umbilicus diameter

### Operculum

Opercular thickness
Opercular colour
Opercular length
* Presence or absence of white smear on inner surface of operculum
Length of white smear
Ratio of opercular length/distance of nucleus from edge of last whorl at half whorl point

### Radula

*Central teeth*
Number of lateral cusps
Ratio of length of central cusp/length of adjacent cusp
* Number of pairs of basal denticles
Shape of dorsal edge
Shape of basal process
Thickness of lateral edge
Extension of lateral edges ventrally

*Lateral teeth*
Cusp formula
Ratio of length of primary cusp/length of adjacent outer cusp
Basal bulge
* Outer shaft - number of times longer than cutting edge

*Marginal teeth*
Cusps
1. inner marginal teeth with larger cusps than outer marginal teeth
2. inner and outer marginal teeth with cusps about equal in strength

### External Features – Head-Foot

* Cephalic tentacles – cross sectional shape
* Dorsal ciliation of cephalic tentacles
* Ventral ciliation of cephalic tentacles
Pigmentation of head foot
Pigmentation of visceral coil

### Pallial Cavity

Number of ctenidial filaments
Position of ctenidial apex
* Position of osphradium relative to posterior end of ctenidium
* Hypobranchial gland
* Presence or absence of glandular pad to left of ctenidium
Presence or absence of glandular pad near anus
Rectal arch present or absent
Position of anus relative to mantle edge [near mantle edge, well back (i.e. about one third of length of pallial cavity from mantle edge), or intermediate between these two positions]
Renal organ (kidney) – extent of protrusion into mantle roof

### Male Reproductive System

* Presence or absence of penial lobes
* Distal portion of penis wrinkled or smooth
Shape of distal end of penis
Pigmentation of penis
* Pallial vas deferens coiled or straight; location of coils, if present.

### Female Reproductive System

* Ventral channel of pallial oviduct simple or modified as vestibule
Position of seminal receptacle relative to bursa copulatrix
Point of origin of bursal duct from bursa copulatrix
Shape and size (relative to albumen gland) of bursa copulatrix
* Fusion of oviduct and bursal duct
* Loops of coiled oviduct
* Shape of oviduct opening
* Presence or absence, and position, of papilla with pallial opening
* Rudimentary penis present or absent in females

Table 2. Characters used in the phylogenetic analysis. The data used in the analysis is given in Table 8 and the character numbers given here correspond to the character numbers given in that table. Characters are ordered unless otherwise noted. An asterisk (*) indicates those character states considered to be plesiomorphic.

SHELL
1. Number of protoconch whorls
   * A. with more than 1.6 whorls
   B. with less than 1.6 whorls.

OPERCULUM
2. Presence or absence of pegs
   * A. with pegs
   B. without pegs (white smear present or absent)

RADULA
3. Number of pairs of basal denticles
   * A. more than two
   B. two or less
4. Outer shaft – number of times longer than cutting edge
   * A. more than 1.5 times as long
   B. less than 1.5 times as long

HEAD-FOOT
5. Cephalic tentacles
   * A. oval to circular in section
   B. triangular in section
6. Dorsal ciliation of cephalic tentacles (unordered)
   A. with dorsal ciliated band present on both tentacles
   B. with dorsal ciliated band present on right tentacle only
   C. with no dorsal ciliated bands present
7. Ventral ciliation of cephalic tentacles (unordered)
   A. distinct ciliated band along most of ventral surface
   B. two distinct ciliated bands along most of ventral surface
   C. three ciliated bands along most of ventral surface
   D. cilia not arranged in bands on ventral surface
8. Osphradium
   * A. near middle of ctenidium
   B. between posterior end and middle of ctenidium
   C. near posterior end of ctenidium
9. Hypobranchial gland
   * A. moderately to well developed
   B. very reduced or absent
10. Glandular pad to left of ctenidium
   * A. no glandular pad to left of ctenidium
   B. well-developed glandular pad to left of ctenidium

GENITALIA:MALE
11. Penial lobes
   * A. absent, simple tapering penis
   B. papilla short, distinct lobes present or distinctly swollen area
   C. papilla short, folds or swelling slightly to moderately developed
   D. papilla long, folds or swelling slightly to moderately developed
   E. long folds to distal end of penis
12. Distal end of penis
   * A. simple, tapering, wrinkled when at rest
   B. modified as papilla and/or lobes, not conspicuously wrinkled when at rest
13. Pallial vas deferens
   * A. straight or undulating
   B. with loops/coils

GENITALIA:FEMALE
14. Ventral channel
   * A. unmodified
   B. modified as muscular vestibule
15. Orientation of bursal duct
   * A. runs anteriorly
   B. runs vertically (ventral to bursa) or posteriorly
16. Coiled oviduct and bursal duct (unordered)
   * A. separate to posterior mantle wall
   B. fused to form common duct about halfway to mantle wall from seminal receptacle duct
   C. fused to form common duct just in front of seminal receptacle duct, bursal duct sloped anteriorly
   D. fused to form common duct, bursal duct vertical to sloped posteriorly
17. Coiled oviduct (unordered)
   * A. simple U-shape
   B. basically U-shaped but with extra bend distally
   C. basically U-shaped but with extra bend proximally
   D. basically U-shaped but with extra bend in middle part
18. Relative size of bursa copulatrix
   * A. bursa copulatrix much larger in size than thin-walled seminal receptacle
   B. bursa copulatrix about equal in size to thick-walled seminal receptacle
19. Opening of oviduct
   * A. short (small)
   B. long, slit-like
20. Papilla bearing oviduct opening (unordered)
   * A. not developed
   B. anterior to capsule gland
   C. behind anterior end of capsule gland
21. Rudimentary penis
   * A. absent in females or present in a few females
   B. present in most or all females

Table 3. Shell and opercular measurements of species of *Jardinella*. AA - angle of outer lip of aperture; AL - aperture length; AW - aperture width; BW - body whorl length; CS - length of white smear; CV - convexity ratio; f - females; OL - opercular length; ON - distance of opercular nucleus from opercular edge; m - males; PD - protoconch diameter; PW - number of protoconch whorls; SA - spire angle; SD - standard deviation; SL - shell length; SW - shell width; TW - number of teleoconch whorls; UW - umbilical width; X - mean.

| | | *J. edgbastonensis* | *J. corrugata* | *J. coreena* | *J. pallida* | *J. colmani* | *J. jesswiseae* | *J. zeidlerorum* | *J. acuminata* | *J. carnarvonensis* | *J. exigua* | *J. isolata* | *J. eulo* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| stn. No. | | 72(A) | Z9(A) | Z14 | 73(A) | 71 | 73(A) | Z12 | 73 | Z15 | 93(B) | 21(C) | 11 |
| number | | 22 | 12 | 12 | 22 | 21 | 22 | 15 | 22 | 39 | 33 | 21 | 22 |
| SL (m) | X | 2.80 | 3.66 | 2.72 | 1.41 | 1.66 | 2.08 | 2.57 | 2.91 | 2.06 | 1.45 | 3.05 | 2.36 |
| | SD | 0.21 | 0.27 | 0.17 | 0.05 | 0.04 | 0.21 | 0.09 | 0.29 | 0.12 | 0.12 | 0.13 | 0.22 |
| (f) | X | 2.98 | 3.73 | 2.84 | 1.62 | 1.96 | 2.43 | 2.62 | 3.00 | 2.14 | 1.38 | 3.23 | 2.58 |
| | SD | 0.17 | 0.21 | 0.16 | 0.11 | 0.18 | 0.17 | 0.14 | 0.37 | 0.18 | 0.10 | 0.31 | 0.17 |
| SW (m) | X | 2.43 | 3.44 | 2.27 | 0.86 | 1.11 | 1.18 | 1.19 | 1.12 | 1.81 | 1.52 | 2.05 | 2.46 |
| | SD | 0.17 | 0.11 | 0.11 | 0.03 | 0.06 | 0.08 | 0.03 | 0.07 | 0.15 | 0.10 | 0.14 | 0.19 |
| (f) | X | 2.58 | 3.49 | 2.36 | 0.94 | 1.26 | 1.29 | 1.25 | 1.15 | 1.90 | 1.46 | 2.17 | 2.75 |
| | SD | 0.14 | 0.18 | 0.11 | 0.04 | 0.10 | 0.06 | 0.08 | 0.11 | 0.13 | 0.09 | 0.16 | 0.13 |
| AL (m) | X | 1.58 | 2.29 | 1.48 | 0.60 | 0.77 | 0.84 | 0.92 | 0.84 | 1.13 | 0.89 | 1.49 | 1.42 |
| | SD | 0.12 | 0.25 | 0.10 | 0.02 | 0.03 | 0.08 | 0.01 | 0.07 | 0.11 | 0.07 | 0.08 | 0.13 |
| (f) | X | 1.65 | 2.22 | 1.54 | 0.68 | 0.87 | 0.89 | 0.98 | 0.85 | 1.15 | 0.83 | 1.51 | 1.62 |
| | SD | 0.10 | 0.12 | 0.10 | 0.03 | 0.07 | 0.05 | 0.06 | 0.07 | 0.12 | 0.08 | 0.12 | 0.09 |
| AW (m) | X | 1.42 | 1.73 | 1.37 | 0.60 | 0.74 | 0.75 | 0.79 | 0.78 | 1.07 | 0.84 | 1.30 | 1.30 |
| | SD | 0.11 | 0.12 | 0.07 | 0.03 | 0.04 | 0.06 | 0.03 | 0.05 | 0.09 | 0.06 | 0.05 | 0.10 |
| (f) | X | 1.50 | 1.75 | 1.38 | 0.66 | 0.82 | 0.82 | 0.83 | 0.79 | 1.11 | 0.81 | 1.34 | 1.47 |
| | SD | 0.09 | 0.08 | 0.06 | 0.02 | 0.06 | 0.06 | 0.07 | 0.07 | 0.08 | 0.05 | 0.10 | 0.09 |
| BW (m) | X | 2.15 | 3.31 | 2.22 | 1.12 | 1.35 | 1.46 | 1.56 | 1.61 | 1.74 | 1.28 | 2.49 | 2.02 |
| | SD | 0.38 | 0.25 | 0.12 | 0.03 | 0.02 | 0.14 | 0.05 | 0.12 | 0.11 | 0.10 | 0.09 | 0.19 |
| (f) | X | 2.31 | 3.39 | 2.31 | 1.27 | 1.58 | 1.67 | 1.66 | 1.64 | 1.81 | 1.21 | 2.62 | 2.19 |
| | SD | 0.32 | 0.19 | 0.13 | 0.06 | 0.14 | 0.08 | 0.08 | 0.15 | 0.15 | 0.09 | 0.21 | 0.12 |
| UW (m) | X | 0.33 | 1.07 | 0.27 | 0.06 | 0.09 | 0.03 | 0.00 | 0.00 | 0.25 | 0.27 | 0.41 | 0.34 |
| | SD | 0.05 | 0.03 | 0.06 | 0.03 | 0.03 | 0.01 | 0.00 | 0.00 | 0.07 | 0.03 | 0.09 | 0.07 |
| (f) | X | 0.35 | 1.16 | 0.34 | 0.05 | 0.09 | 0.04 | 0.00 | 0.00 | 0.25 | 0.25 | 0.46 | 0.40 |
| | SD | 0.04 | 0.10 | 0.04 | 0.02 | 0.02 | 0.02 | 0.00 | 0.00 | 0.05 | 0.04 | 0.10 | 0.06 |
| CV (m) | X | 0.26 | 0.32 | 0.28 | 0.19 | 0.22 | 0.20 | 0.12 | 0.09 | 0.25 | 0.26 | 0.19 | 0.22 |
| | SD | 0.03 | 0.02 | 0.02 | 0.04 | 0.04 | 0.03 | 0.02 | 0.03 | 0.03 | 0.05 | 0.03 | 0.02 |
| (f) | X | 0.26 | 0.33 | 0.27 | 0.22 | 0.21 | 0.20 | 0.14 | 0.09 | 0.25 | 0.26 | 0.19 | 0.20 |
| | SD | 0.03 | 0.04 | 0.03 | 0.04 | 0.03 | 0.02 | 0.02 | 0.02 | 0.04 | 0.05 | 0.02 | 0.02 |

Table 3 (cont'd).

| | | *J. edgbastonensis* | *J. corrugata* | *J. coreena* | *J. pallida* | *J. colmani* | *J. jesswiseae* | *J. zeidlerorum* | *J. acuminata* | *J. carnarvonensis* | *J. exigua* | *J. isolata* | *J. eulo* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| stn. No. | | 72(A) | Z9(A) | Z14 | 73(A) | 71 | 73(A) | Z12 | 73 | Z15 | 93(B) | 21(C) | 11 |
| number | | 22 | 12 | 12 | 22 | 21 | 22 | 15 | 22 | 39 | 33 | 21 | 22 |
| SA (m) | X | 83.17 | 91.05 | 79.07 | 73.52 | 82.83 | 57.06 | 44.39 | 36.75 | 95.31 | 103.68 | 71.11 | 100.29 |
| | SD | 3.47 | 2.52 | 2.86 | 2.92 | 3.02 | 3.05 | 2.09 | 3.57 | 7.23 | 7.97 | 3.64 | 4.42 |
| (f) | X | 84.47 | 93.81 | 80.86 | 68.88 | 77.19 | 55.35 | 45.28 | 36.40 | 93.87 | 105.04 | 70.01 | 99.79 |
| | SD | 4.25 | 6.79 | 3.95 | 4.34 | 2.89 | 4.16 | 1.75 | 3.26 | 5.96 | 8.42 | 5.03 | 4.25 |
| AA (m) | X | 20.33 | 23.68 | 23.93 | 21.06 | 12.57 | 19.73 | 4.18 | 6.31 | 30.52 | 27.47 | 11.13 | 27.94 |
| | SD | 4.12 | 0.91 | 2.70 | 4.54 | 4.35 | 5.74 | 3.86 | 2.32 | 3.67 | 4.46 | 3.76 | 3.52 |
| (f) | X | 22.18 | 24.72 | 21.12 | 16.71 | 15.74 | 20.16 | 3.95 | 5.16 | 31.43 | 29.58 | 13.36 | 24.15 |
| | SD | 2.41 | 3.64 | 4.09 | 3.37 | 4.95 | 4.06 | 2.00 | 2.12 | 4.97 | 4.00 | 4.80 | 3.50 |
| PD (m) | X | 0.41 | 0.37 | 0.44 | 0.30 | 0.39 | 0.34 | 0.33 | 0.30 | 0.42 | 0.39 | 0.43 | 0.43 |
| | SD | 0.03 | 0.01 | 0.02 | 0.03 | 0.02 | 0.03 | 0.01 | 0.02 | 0.03 | 0.04 | 0.03 | 0.03 |
| (f) | X | 0.42 | 0.38 | 0.45 | 0.32 | 0.40 | 0.34 | 0.31 | 0.31 | 0.43 | 0.40 | 0.45 | 0.43 |
| | SD | 0.03 | 0.04 | 0.03 | 0.03 | 0.04 | 0.02 | 0.02 | 0.02 | 0.03 | 0.03 | 0.06 | 0.03 |
| PW (m) | X | 1.31 | 1.28 | 1.25 | 1.24 | 1.26 | 1.26 | 1.25 | 1.39 | 1.24 | 1.26 | 1.27 | 1.29 |
| | SD | 0.10 | 0.03 | 0.00 | 0.02 | 0.04 | 0.05 | 0.00 | 0.07 | 0.02 | 0.04 | 0.02 | 0.02 |
| (f) | X | 1.35 | 1.26 | 1.26 | 1.24 | 1.27 | 1.25 | 1.26 | 1.40 | 1.25 | 1.27 | 1.28 | 1.28 |
| | SD | 0.06 | 0.04 | 0.02 | 0.03 | 0.03 | 0.05 | 0.02 | 0.08 | 0.01 | 0.05 | 0.04 | 0.05 |
| TW (m) | X | 2.99 | 2.80 | 2.85 | 2.25 | 2.20 | 3.20 | 4.15 | 5.00 | 2.51 | 1.87 | 2.91 | 2.64 |
| | SD | 0.15 | 0.07 | 0.27 | 0.06 | 0.15 | 0.17 | 0.14 | 0.38 | 0.12 | 0.16 | 0.22 | 0.15 |
| (f) | X | 3.03 | 2.79 | 2.93 | 2.45 | 2.45 | 3.55 | 4.05 | 4.92 | 2.57 | 1.93 | 2.81 | 2.73 |
| | SD | 0.14 | 0.06 | 0.13 | 0.09 | 0.08 | 0.22 | 0.20 | 0.34 | 0.16 | 0.15 | 0.21 | 0.14 |
| OL (m) | X | 1.36 | 1.93 | 1.26 | 0.63 | 0.75 | 0.80 | 0.76 | 0.69 | 0.97 | 0.83 | 1.41 | 1.29 |
| | SD | 0.08 | 0.14 | 0.03 | 0.03 | 0.03 | 0.06 | 0.01 | 0.06 | 0.07 | 0.06 | 0.07 | 0.10 |
| (f) | X | 1.45 | 1.97 | 1.31 | 0.70 | 0.85 | 0.88 | 0.79 | 0.73 | 1.01 | 0.80 | 1.46 | 1.46 |
| | SD | 0.09 | 0.09 | 0.06 | 0.04 | 0.07 | 0.04 | 0.05 | 0.06 | 0.08 | 0.05 | 0.09 | 0.08 |
| ON (m) | X | 0.42 | 0.61 | 0.37 | 0.19 | 0.25 | 0.21 | 0.19 | 0.16 | 0.32 | 0.28 | 0.43 | 0.43 |
| | SD | 0.03 | 0.13 | 0.01 | 0.02 | 0.01 | 0.02 | 0.02 | 0.03 | 0.03 | 0.03 | 0.04 | 0.03 |
| (f) | X | 0.44 | 0.60 | 0.41 | 0.22 | 0.28 | 0.24 | 0.20 | 0.17 | 0.33 | 0.28 | 0.45 | 0.47 |
| | SD | 0.03 | 0.08 | 0.03 | 0.02 | 0.04 | 0.03 | 0.02 | 0.02 | 0.04 | 0.03 | 0.04 | 0.04 |
| CS (m) | X | 0.15 | 0.33 | 0.00 | 0.13 | 0.00 | 0.00 | 0.26 | 0.33 | 0.00 | 0.00 | 0.52 | 0.27 |
| | SD | 0.10 | 0.17 | 0.00 | 0.06 | 0.00 | 0.00 | 0.04 | 0.06 | 0.00 | 0.00 | 0.08 | 0.10 |
| (f) | X | 0.24 | 0.42 | 0.00 | 0.15 | 0.04 | 0.00 | 0.30 | 0.34 | 0.00 | 0.00 | 0.53 | 0.26 |
| | SD | 0.25 | 0.24 | 0.00 | 0.11 | 0.11 | 0.00 | 0.07 | 0.08 | 0.00 | 0.00 | 0.13 | 0.10 |

Table 4. The distribution of hydrobiids and *Gabbia* sp. in the Edgbaston Springs. Percentage frequencies are given except for the undescribed hydrobiid species (which is known from only one shell) and *Gabbia*.

| | *edgbastonensis* | *acuminata* | *jesswiseae* | *pallida* | *corrugata* | n.sp. | *Gabbia* |
|---|---|---|---|---|---|---|---|
| Station 73 | | | | | | | |
| Head of spring | – | – | 100.0 | – | – | – | – |
| Upper outflow | – | 11.3 | 76.0 | 12.7 | – | * | * |
| Lower outflow | 2.1 | 21.2 | 67.5 | 2.1 | 7.0 | – | * |
| Small seep | 51.2 | – | 18.9 | 1.4 | 28.6 | – | – |
| Station 72 | | | | | | | |
| Head of spring | – | – | 47.4 | 52.6 | – | – | – |
| Middle of middle outflow | – | – | 84.2 | 15.8 | – | – | – |
| Edge of middle outflow | 71.4 | – | 9.4 | 19.2 | – | – | * |
| Lower outflow | 54.4 | – | 4.8 | 40.8 | – | – | * |

Table 5. Comparisons of generalised distances between groups (species) generated by discriminate analysis.

| | *J. edgbastonensis* | *J. acuminata* | *J. colmani* | *J. eulo* | *J. corrugata* | *J. pallida* | *J. exigua* | *J. carnarvonensis* | *J. coreena* | *J. jesswiseae* | *J. zeidlerorum* | *J. isolata* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *J. edgbastonensis* | 0.000 | 21.649 | 11.417 | 5.188 | 17.817 | 13.911 | 8.523 | 5.722 | 3.226 | 13.249 | 16.159 | 9.422 |
| *J. acuminata* | 21.649 | 0.000 | 16.959 | 24.326 | 34.478 | 16.394 | 21.457 | 19.804 | 21.111 | 11.293 | 7.431 | 20.498 |
| *J. colmani* | 11.417 | 16.959 | 0.000 | 14.004 | 24.936 | 3.543 | 7.168 | 7.111 | 9.788 | 6.148 | 10.405 | 9.363 |
| *J. eulo* | 5.188 | 24.326 | 14.004 | 0.000 | 18.419 | 16.443 | 9.468 | 7.252 | 6.405 | 16.096 | 19.091 | 12.766 |
| *J. corrugata* | 17.817 | 34.378 | 24.936 | 18.419 | 0.000 | 26.555 | 21.211 | 20.631 | 18.282 | 27.468 | 29.875 | 17.580 |
| *J. pallida* | 13.911 | 16.394 | 3.543 | 16.443 | 26.555 | 0.000 | 8.912 | 9.758 | 12.589 | 6.228 | 10.101 | 11.547 |
| *J. exigua* | 8.523 | 21.457 | 7.168 | 9.468 | 21.211 | 8.912 | 0.000 | 4.448 | 7.740 | 11.359 | 15.488 | 10.643 |
| *J. carnarvonensis* | 5.722 | 19.804 | 7.111 | 7.252 | 20.631 | 9.758 | 4.448 | 0.000 | 4.118 | 9.937 | 13.745 | 8.892 |
| *J. coreena* | 3.226 | 21.111 | 9.788 | 6.405 | 18.282 | 12.589 | 7.740 | 4.118 | 0.000 | 11.978 | 15.162 | 7.797 |
| *J. jesswiseae* | 13.249 | 11.293 | 6.148 | 16.096 | 27.468 | 6.228 | 11.359 | 9.937 | 11.978 | 0.000 | 4.711 | 12.029 |
| *J. zeidlerorum* | 16.159 | 7.431 | 10.405 | 19.091 | 29.875 | 10.101 | 15.488 | 13.745 | 15.162 | 4.711 | 0.000 | 14.667 |
| *J. isolata* | 9.422 | 20.498 | 9.363 | 12.766 | 17.580 | 11.547 | 10.643 | 8.892 | 7.797 | 12.029 | 14.667 | 0.000 |

Table 6. Euclidean (=Taxonomic) distances between groups (species) generated by discriminate analysis.

| | *J. edgbastonensis* | *J. acuminata* | *J. colmani* | *J. eulo* | *J. corrugata* | *J. pallida* | *J. exigua* | *J. carnarvonensis* | *J. coreena* | *J. jesswiseae* | *J. zeidlerorum* | *J. isolata* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *J. edgbastonensis* | 0.000 | 2.622 | 2.099 | 0.567 | 1.979 | 2.638 | 2.469 | 1.289 | 0.258 | 1.798 | 1.925 | 0.641 |
| *J. acuminata* | 2.622 | 0.000 | 2.832 | 2.921 | 4.137 | 3.011 | 3.486 | 2.705 | 2.607 | 1.708 | 0.989 | 2.699 |
| *J. colmani* | 2.099 | 2.832 | 0.000 | 1.844 | 3.905 | 0.574 | 0.771 | 0.865 | 1.903 | 1.133 | 1.875 | 2.165 |
| *J. eulo* | 0.567 | 2.921 | 1.844 | 0.000 | 2.214 | 2.376 | 2.070 | 0.985 | 0.526 | 1.813 | 2.121 | 0.998 |
| *J. corrugata* | 1.979 | 4.137 | 3.905 | 2.214 | 0.000 | 4.456 | 4.153 | 3.098 | 2.106 | 3.691 | 3.693 | 1.901 |
| *J. pallida* | 2.638 | 3.011 | 0.574 | 2.376 | 4.456 | 0.000 | 0.814 | 1.398 | 2.451 | 1.399 | 2.115 | 2.720 |
| *J. exigua* | 2.469 | 3.486 | 0.771 | 2.070 | 4.153 | 0.814 | 0.000 | 1.212 | 2.295 | 1.808 | 2.541 | 2.618 |
| *J. carnarvonensis* | 1.289 | 2.705 | 0.865 | 0.985 | 3.098 | 1.398 | 1.212 | 0.000 | 1.105 | 1.154 | 1.753 | 1.468 |
| *J. coreena* | 0.258 | 2.607 | 1.903 | 0.526 | 2.106 | 2.451 | 2.295 | 1.105 | 0.000 | 1.657 | 1.851 | 0.553 |
| *J. jesswiseae* | 1.798 | 1.708 | 1.133 | 1.813 | 3.691 | 1.399 | 1.808 | 1.154 | 1.657 | 0.000 | 0.749 | 1.899 |
| *J. zeidlerorum* | 1.925 | 0.989 | 1.875 | 2.121 | 3.693 | 2.115 | 2.541 | 1.753 | 1.851 | 0.749 | 0.000 | 2.020 |
| *J. isolata* | 0.641 | 2.699 | 2.165 | 0.998 | 1.901 | 2.720 | 2.618 | 1.468 | 0.553 | 1.899 | 2.020 | 0.000 |

Table 7. Percentage of the variance of each variable in each canonical variate from a canonical analysis of discriminance. AL – aperture length; BW – body whorl length; CV – convexity ratio; PD – protoconch diameter; PW – number of protoconch whorls; SL – shell length; SW – shell width; TW – number of teleoconch whorls; UW – umbilical width.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| SL | 60.330 | 0.327 | 31.706 | 6.094 | 0.620 | 0.637 | 0.058 | 0.006 | 0.221 |
| SW | 83.066 | 4.058 | 12.716 | 0.070 | 0.000 | 0.006 | 0.039 | 0.037 | 0.008 |
| AL | 45.156 | 47.269 | 4.643 | 1.057 | 0.378 | 0.007 | 0.230 | 1.094 | 0.166 |
| BW | 1.873 | 1.386 | 55.416 | 13.632 | 9.686 | 6.441 | 4.915 | 4.725 | 1.928 |
| UW | 54.776 | 32.822 | 7.675 | 4.561 | 0.115 | 0.005 | 0.028 | 0.020 | 0.000 |
| CV | 91.832 | 4.999 | 0.467 | 0.307 | 0.762 | 0.773 | 0.781 | 0.078 | 0.000 |
| PD | 12.934 | 3.341 | 62.198 | 9.527 | 7.064 | 1.409 | 3.010 | 0.492 | 0.025 |
| PW | 38.222 | 26.624 | 5.324 | 19.408 | 0.114 | 8.406 | 1.093 | 0.537 | 0.271 |
| TW | 73.437 | 18.382 | 6.873 | 1.062 | 0.064 | 0.164 | 0.007 | 0.003 | 0.008 |

Table 8. Data used in the phylogenetic analysis. The characters (1–21) and character states (A–E) are listed in Table 2 (Note:- *J. thaanumi* was ommited from the primary analysis).

| Characters | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Unordered char.(*) | | | * | * | | | | | | | | | | | | * | * | | | * | |
| *Tatea* | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A | A |
| *Fluvidona* | B | A | A | A | A | A | C | B | A | A | A | A | A | A | A | A | ? | A | A | A | A |
| *Fonscochlea* | B | A | B | B | A | C | A | C | B | A | A | A | A | A | B | D | B | B | A | A | A |
| *J. thaanumi* | B | B | B | A | ? | C | A | B | A | A | D | B | B | A | A | A | A | A | A | A | A |
| *J. edgbastonensis* | B | B | B | A | A | C | A | B | B | A | D | B | B | B | A | A | A | A | A | B | A |
| *J. corrugata* | B | B | B | A | B | B | C | A | B | A | E | B | B | B | A | A | A | A | A | B | A |
| *J. coreena* | B | B | B | A | B | C | D | B | B | A | E | B | B | B | A | A | B | A | A | B | A |
| *J. pallida* | B | B | B | A | B | A | C | B | A | A | D | B | B | B | A | B | B | A | A | C | A |
| *J. colmani* | B | B | B | B | B | B | C | B | B | A | D | B | B | B | A | B | D | A | A | C | A |
| *J. jesswiseae* | B | B | B | A | B | B | B | B | A | A | C | B | B | B | A | A | A | A | A | A | A |
| *J. zeidlerorum* | B | B | B | A | B | B | D | B | A | B | D | B | B | A | A | B | A | A | A | A | A |
| *J. acuminata* | B | B | B | ? | B | C | A | B | A | B | D | B | B | A | A | B | A | A | B | A | A |
| *J. carnarvonensis* | B | B | B | A | B | C | D | A | B | A | C | B | B | B | A | A | A | A | B | A | B |
| *J. exigua* | B | B | B | A | B | C | B | B | B | A | C | B | B | A | ? | ? | A | A | B | A | B |
| *J. isolata* | B | B | B | A | A | A | A | B | A | A | B | B | A | A | A | C | C | A | A | A | A |
| *J. eulo* | B | B | B | A | A | C | A | B | B | A | B | B | A | A | A | C | C | A | A | A | A |

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# Additions to the Ascothoracidan Fauna of Australia and South-east Asia (Crustacea, Maxillopoda): Synagogidae (part), Lauridae and Petrarcidae

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ABSTRACT. Previous Australian records of Ascothoracida are summarised. In the Synagogidae, three new species of *Gorgonolaureus* Utinomi are described from primnoid (*Pterostenella plumatilis* (Rousseau)), paramuriceid (unidentified), and gorgoniid (*Eunicella* sp.) gorgonacean hosts off Western Australia, Vietnam, and New Caledonia, respectively. The first two species are from unusually shallow depths, 80 to 100 m, the third from bathyal depths. *Flatsia* n.gen., with one species from 73 to 82 m depth off New South Wales, host unknown, is provisionally assigned to the Synagogidae. In the Lauridae, two new species of *Baccalaureus* Broch are described from the subtidal zoanthid *Isaurus tuberculatus* Gray on the Great Barrier Reef and the solitary zoanthid *Sphenopus marsupialis* Steenstrup at several shallow sites (40–86 m) off Queensland and Western Australia and in the Andaman Sea. In the Petrarcidae, morphological and ecological notes on *Petrarca okadai* Grygier infesting the coral *Heteropsammia cochlea* (Spengler) at Lizard Island, Queensland, are presented. Two new species of *Petrarca* Fowler are described infesting the solitary coral *Fungiacyathus* sp. off Moreton Bay, Queensland, and the hermatypic reef coral *Turbinaria reniformis* Bernard at Lizard Island. An unnamed species of *Petrarca* from the solitary coral *Anthemiphyllia dentata* Alcock collected between 110 and 350 m off Queensland is partly described. A list and some photographs of other new records of galls caused by petrarcid ascothoracidans in various Indo-Pacific scleractinians, especially *Turbinaria* spp. and other dendrophylliids, are presented.

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The superorder Ascothoracida encompasses a diversity of parasitic crustaceans, the hosts of which include members of the echinoderm classes Asteroidea, Crinoidea, Echinoidea and Ophiuroidea, and anthozoans belonging to the Scleractinia, Zoanthidea, Gorgonacea, Alcyonacea and Antipatharia. Wagin (1976) published the most recent comprehensive review of the group, although since then the number of described species has more than doubled to about 90. Grygier (1987c) published an updated classification of the Ascothoracida, with two orders and six families, and summarised some of the morphological characteristics of the different genera in tabular form. This superorder, together with the Cirripedia and Facetotecta, is considered part of the maxillopodan subclass Thecostraca (Grygier, 1987b).

By 1986, several varieties of Ascothoracida were already known from Australian waters. Bernard (1896) described apparent petrarcid galls in *Turbinaria edwardsi* Bernard from north-western Australia but did not recognise them as such (cited by Zibrowius & Grygier, 1985). Pyefinch (1937) described the laurid *Baccalaureus torrensis* infesting the zoanthid *Palythoa howesii* Haddon & Shackleton at Thursday Island in the Torres Straits. Hickman (1959) described in good detail the dendrogastrid *Dendrogaster tasmaniensis* infesting the asteroid *Allostichaster polyplax* Müller & Troschel in south-eastern Tasmania. Kenny (1959) briefly noted another *Dendrogaster*, identified by him as *Myriocladus ludwigi* (le Roi), from the asteroid *Nepanthia belcheri* (Perrier) in Moreton Bay, Queensland. Zann (1980) showed a photograph of an unidentified *Dendrogaster*, host unspecified, and stated that an ascothoracidan parasite was known in the crown-of-thorns starfish *Acanthaster planci* (Linnaeus). Dr L.R.G. Cannon of the Queensland Museum (personal communication), the supposed source of the latter information (Zann, personal communication), assures me that it is a mistake and no such parasite is known; the true provenance of Zann's illustrated *Dendrogaster* is unclear. Grygier (1981) described the petrarcid *Petrarca okadai* infesting the coral *Heteropsammia michelini* Milne Edwards & Haime (i.e., *H. cochlea* (Spengler)) from Lizard Island, Queensland, based on specimens collected by Fisk (1981). Fisk also reported what may be the same parasite from *Heterocyathus aequicostatus* Milne Edwards & Haime at Lizard Island, and from both corals at Wistari Reef near Heron Island, Queensland (cited by Zibrowius & Grygier, 1985). Lowry (1985) described the synagogid *Cardomanica andersoni* from the deep-water gorgonian *Chrysogorgia orientalis* Versluys in the Tasman Sea and Muirhead & Ryland (1985) reported a possible *Baccalaureus* infesting the zoanthid *Isaurus tuberculatus* Gray on the Great Barrier Reef near Townsville, Queensland.

In 1987 I had the opportunity to visit most of the natural history museums of Australia in order to work up previously culled ascothoracidans, to screen collections of echinoderms and anthozoans for previously unnoticed forms, and to collect ascothoracidans in the field at the Lizard Island Research Station. The present report concerns the representatives of the families Lauridae and Petrarcidae and part of the Synagogidae that were discovered during that visit, together with other representatives of these taxa from nearby regions that came to me from other sources. All are members of the order Laurida. A preliminary report on my new findings of Australian Ctenosculidae and Dendrogastridae (order Dendrogastrida) has already been published (Grygier, 1988a), and the crinoid-infesting synagogid genus *Waginella* has also been treated elsewhere (Grygier, 1990a). I intend to treat the remaining portion of the Synagogidae, comprising several new species provisionally but unsatisfactorily attributed to the genus *Thalassomembracis* Grygier, together with similar forms from various European museums, in the context of a cladistic revision of all the gorgonian-infesting Ascothoracida.

All tables referred to throughout the text are in Appendix 1.

## Synagogidae Gruvel, 1905

### *Gorgonolaureus* Utinomi, 1962

### *Gorgonolaureus decurvatus* n.sp.

Figs 1, 2, Tables 1, 2

**Type material.** HOLOTYPE and 9 PARATYPE females (Western Australian Museum, WAM 93-87) occupying polyp-covered cysts (Fig. 1A) on single colony (1 of 3 in

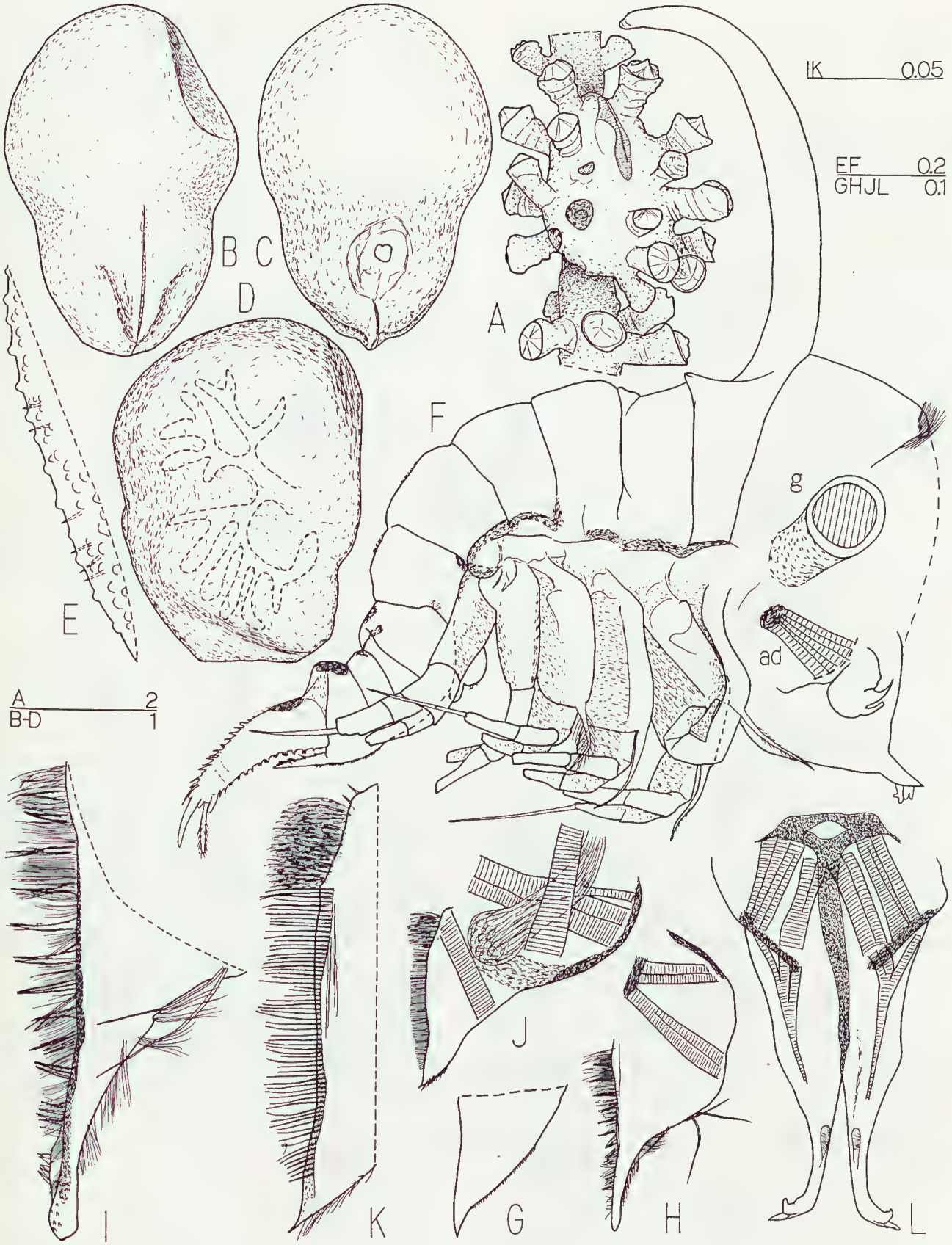


**Fig.1.** *Gorgonolaureus decurvatus* n.sp. (WAM 93-87). A, paratype #5 *in situ*. B, holotype, rear view. C–D, paratype #5, front and lateral views, latter with superimposed gut diverticulum of paratype #2 (dashed). E, lip of carapace aperture. F, body of paratype #1. G–L, mouthparts of paratype #1: G, medial languette; H–I, mandible and enlargement of its distal part; J–K, maxillule and enlargement of its medial edge; L, maxillae. Abbreviations: ad; adductor muscle; g, gut diverticulum. Scale bars in mm.

**Fig.2.** *Gorgonolaureus decurvatus* n.sp. (WAM 93-87). A, right antennule of paratype #1, medial view. B–F, thoracopods of paratype #2: B, composite of both thoracopods I; C, right II; D, left III; E, V (side uncertain); F, left VI; C–E with seminal receptacles in coxae, numbers in B,D,F corresponding to usage in Tables 2-5. G, abdomen of paratype #1 with penis, right telsonic spine, and right furcal ramus; H, furcal rami and right telsonic spine (left one absent) of paratype #2. Scale bars in mm.

jar) of gorgonian *Pterostenella plumatilis* (Rousseau) (WAM 12-87, determined by P. Alderslade), J. Marshall, F/V *Soela*, Stn SO 4B/82/64, 17 July 1982, 42.6 km east-north-east of Glomar Shoal, north-north-east of Dampier, WA, 19°25-26.6'S, 117°11-12.4'E, 98-90 m. 2 paratypes fully dissected, 2 others and holotype partly dissected to expose main body.

**Diagnosis.** Carapace of adult females less than 2.5 mm high, length 70-75% of height. Aperture margins lined with papillae, ventral half of carapace with external papillae and spinules; separate aperture for oral cone low on anterior side. Gut diverticulum on each side bifurcate, each branch with several side branches. Naked dorsal horn on thoracomere 2. Antennules very spinose, segment 5 with about 7 setae, segment 6 about as long as segment 5, with proximal sensory complex directly behind claw guard and aesthetasc of former standing separately. Thoracopods reaching farther ventrally than oral cone, with 7-9 setae on each distal exopod segment, 3-4 on each distal endopod segment, usually 2 ampoule-shaped seminal receptacles each in thoracopods II-V. Posteroventral telsonic spines over one third as long as furcal rami, latter tapered and strongly curved ventrally, with 3 short terminal setae, 1 subterminoventral seta, 7-11 short, thin, medial setae, and clusters of blunt spines along ventral margin.

**Description of females** (based principally on 2 paratypes). Dimensions of 5 specimens given in Table 1. Carapace univalved, with posteroventral, slit-like aperture along midline and separate small opening for oral cone near base of anterior midline (Fig.1B,C); rounded in front and rear view, with bulbous dorsal brood chamber atop narrower body chamber; oblong in side view, with nearly straight anterior side, rounded dorsum, and oblique posteroventral side surmounted by slight protrusion marking posterior end of aperture (Fig.1D). Aperture margins bearing small papillae and few short internal guard setae (Fig.1E); similar papillae on posteroventral outer surface, changing gradually into spinules farther dorsally and then disappearing. Lateral gut diverticulum in each half of carapace consisting of bifurcating dorsal branch and curved ventral branch with posteroventral side branches, ovary diverticulum relatively small, partly surrounding adductor muscle tentorium.

Main body (Fig.1F) attached anteroventrally within carapace and occupying its ventral third. Body of smaller dissected paratype 1.30 mm long from front of oral cone to tips of furcal rami. Body consisting of head with antennules and oral cone, 6-segmented thorax with dorsal horn on second segment and 6 pairs of biramous thoracopods reaching farther ventrally than oral cone, and 5-segmented abdomen with vestigial penis, posteroventral telsonic spines, and furcal rami. No eyes or frontal filament complexes observed. Thoracomeres nearly all of same length, transverse band of setae across front of slightly longer first segment; no filamentary appendages associated with first pair of thoracopods; dorsal horn naked, lightly curved posteriorly especially at tip, relative length of horn somewhat variable but generally slightly shorter than thoracic dorsum; pair of small, lateral epaulets on sixth segment. Abdominal segments all shorter than high, especially third and fourth.

Description of antennule based on right ones of 2 paratypes. Six-segmented, reaching to midlength of oral cone when folded (Figs 1F, 2A). First segment triangular, unarmed; second parallelogram-shaped with patches of long cuticular ctenae; third triangular, bearing numerous long, hair-like setae along anterior edge; fourth segment short, rectangular, with 2 short, spinulose setae and several spinules on anterior edge; fifth one nearly right triangular, with 6 or 7 short, spinulose setae along proximal two thirds of anterior edge and short cuticular ctenae posteriorly. Sixth segment little shorter than fifth, slightly curved and distally broadened to bear large, movable claw; surfaces heavily armed with spinules, 3 short setae clearly seen at base of claw in one specimen; robust claw guard with lateral flange and at least 2 apical setae (tip obscured in both preparations); short, cylindrical proximal sensory process with 3 setae directly behind claw guard, followed by separate short aesthetasc.

Oral cone triangular in cross section and in side view, tip produced into long, hypodermic needle-like point (Fig.1F). Labrum forming outer sheath of cone, lateral margins meeting and locked together behind other mouthparts. Medial languette triangular with minute hairs along anterior edge (Fig.1G). Mandible (Fig.1H,I) with broad, flat, muscular base narrowing to thin, bluntly pointed process; lateral edge with several long hairs and, farther distally, many shorter ones; medial edge with dense, fine hairs interspersed between regularly spaced clumps of thicker, spine-like hairs; tip with few minute, hook-like denticles. Maxillule (Fig.1J,K) with broad, muscular base containing nervous ganglion, and triangular distal part similar in shape and size to medial languette; lateral edge with few distal hairs, medial edge with mat of extremely fine hairs basally and about 63 comb setae along rest of edge, with web-like connection between setal bases. Maxillae fused basally, but distal 40% free, bifid tips bent laterally, ventral points somewhat hook-shaped (Fig.1L).

Thoracopods subequal in length, but second pair longest, others becoming slightly shorter towards rear (Fig.2B-F). Coxa longer than wide in thoracopods I and VI, trapezoidal and about as long as basal width in other pairs. Basis square or slightly shorter than wide except relatively longer in thoracopod I. Exopods 2-segmented with second segment slightly or moderately longer than first. Endopods shorter than exopods, 2-segmented in thoracopods I and VI, otherwise 3-segmented except aberrantly 2-segmented in one thoracopod III of paratype 2. Extensive lining of dense, fine hairs along margins of pairs II-IV, less on I and V, few on VI; cuticular ctenae also present, especially medially (mostly not illustrated). Setation of paratype 1 given in Table 2; terminal setae about as long as rami, and exopods of thoracopods II-VI with 3 apical setae, endopods with 2. Setation of paratype 2 similar except lateral coxal seta

unilaterally present on thoracopod V (position 1), 3-4 medial coxal setae present on thoracopods II and III (position 9), and no seta on proximal endopod segment of thoracopod I (position 6+7). All setae plumose except setules very short on thoracopod I. Two (occasionally 1) ampoule-shaped seminal receptacles each in thoracopods II-V, occupying lateral half of coxa, some of them empty (Fig.2C-E).

Abdominal segments 2-5 with many ventral cuticular ctenae (Fig.2G). Small penis rudiment on first segment reaching to end of second (Fig.2G); shaft with cuticular ctenae and in one specimen ending in small distal spine; rami short, unarmed. Telsonic spines with at least 2 rows of distally pointing spinules on dorsal side (Fig.2G,H). Furcal rami about as long as last 4 abdominal segments combined, basal height about half that of telson; rami curved downwards, tapering, about 2.5 times longer than basal height (Fig.2G,H). Three short terminal setae, naked middle one much shorter than spinulose others (one of latter missing on right side of paratype 2). Short, spinulose, subterminal seta on ventral edge. Row of short, very thin, simple setae along upper half of medial face, 10-11 in paratype 1, 7 in paratype 2. Ventral edge with about 15 clusters of short, rounded spines; dorsal margin, proximodorsal part of medial face, and distal part of lateral face set with cuticular ctenae; ventral half of medial face with small spinules proximally and pores more distally.

**Nauplii.** Four of 5 dissected specimens brooding eggs or nauplii, brood sizes about 20-50 (Table 1). Size and morphological details of nauplii difficult to determine due to larval retention of 2 unshed exuviae in one brood and at least 4 in another, but outermost cuticle averaging 442 µm long in those from paratype 2, living tissue averaging 384 µm (n = 25). Setation described following conventions of Grygier (1987a). On outermost cuticle of antennule, corresponding perhaps to instar I, proximal medial setae 'a' and 'b' not confirmed; of subapical setae, lateral 'd' longer than medial 'f', 'e' absent; most lateral of 3 apical 'g' setae a mere spine. Antennal exopod with 5 setae, mandibular exopod with 4 setae, endopodal setation of both limbs 0?-1-2, protopods obscured.

**Remarks.** *Gorgonolaureus decurvatus* n.sp. is quite similar to the type species, *G. bikiniensis* Utinomi, as redescribed by Grygier (1981c). Unfortunately, the mouthparts and some of the thoracopodal setation of the latter remain unknown. These species are the same size and have papillose margins of the carapace aperture and bifurcate gut diverticula (latter simpler in *G. bikiniensis*). Both have the fifth and sixth antennular segments nearly equally long, similar setation on the fifth segment, and the proximal sensory complex directly behind the claw guard. The setal counts of the distal segments of the thoracopodal rami usually differ by no more than 2, and both species have 2 seminal receptacles each in thoracopods II to V (interpreted as bilobed sacs in *G. bikiniensis*: Grygier, 1981c) and rather long, tapered furcal rami with a few distal setae and several medial ones, all setae short. In contrast, adult females of the other previously described species in this genus, *G. muzikae* Grygier (1981b), have a carapace over 5 mm high with distinctly scalloped aperture margins and highly branched gut diverticula. The sixth segment of the antennule is markedly shorter than the fifth, with about 12 setae on the fifth segment and the proximal sensory complex separated from the claw guard. *Gorgonolaureus muzikae* has about twice as many setae as *G. decurvatus* on the distal segments of the rami of thoracopods II to VI, clusters of 10 to 20 seminal receptacles in thoracopods II to V, and rectangular furcal rami with much more numerous, relatively longer setae.

Numerous differences from *G. bikiniensis* justify *G. decurvatus* as a new species. The former has spinules over the whole carapace, not just the ventral half, and its dorsal brood chamber is more spherical. The antennules of *G. bikiniensis* are not especially spinose, the claw is shorter and stouter, and the aesthetasc arises from the proximal sensory process proper. The dorsal horn has some long hairs and no band of setae was reported on the first thoracomere, although the latter may have been overlooked. The thoracopods and oral cone reach to about the same level in *G. bikiniensis*, the telsonic spines are small, and the furcal rami are straight, with the medial setae similar to the terminal ones.

The brooded nauplii of both previously described species of *Gorgonolaureus* are nearly twice as large as here (0.6-0.8 mm) but do retain a series of unshed exuviae like the present ones (Grygier, 1981c, 1987a). At least five instars could be demonstrated in *G. muzikae*, and that number also seems to be valid for *G. decurvatus*. Some short setae present in instar I nauplii of *G. muzikae* were not found here (cf. Grygier, 1981a: fig.2).

*Gorgonolaureus bikiniensis* was found on the paramuriceid gorgonian *Paracis squamata* (Nutting) at about 220 m at Bikini Atoll in the Marshall Islands, and *G. muzikae* infests an undescribed paramuriceid of uncertain generic affinity from about 366 m off Oahu, Hawaii. *Gorgonolaureus decurvatus* from north-western Australia represents a significant range extension of the genus into the Indian Ocean, and a much shallower depth of occurrence (90-98 m) than any reported until now for the four known genera of gorgonian-inhabiting ascothoracidans (previous records at 220 to 2000 m, but see *G. vietnamianus* n.sp. below). The host gorgonian, *Pterostenella plumatilis*, belongs to the Primnoidae, and is the first ascothoracidan host known in that family.

**Etymology.** Named for the decurved furcal rami.

### *Gorgonolaureus vietnamianus* n.sp.

Figs 3–5, Table 3

**Type material.** HOLOTYPE female (Zoological Institute, Leningrad, ZIN 1/66583) and PARATYPE female (ZIN 2/66584), both brooding nauplii and dissected at least unilaterally. Encysted by numerous polyps at different sites on same 65 mm high and wide colony of

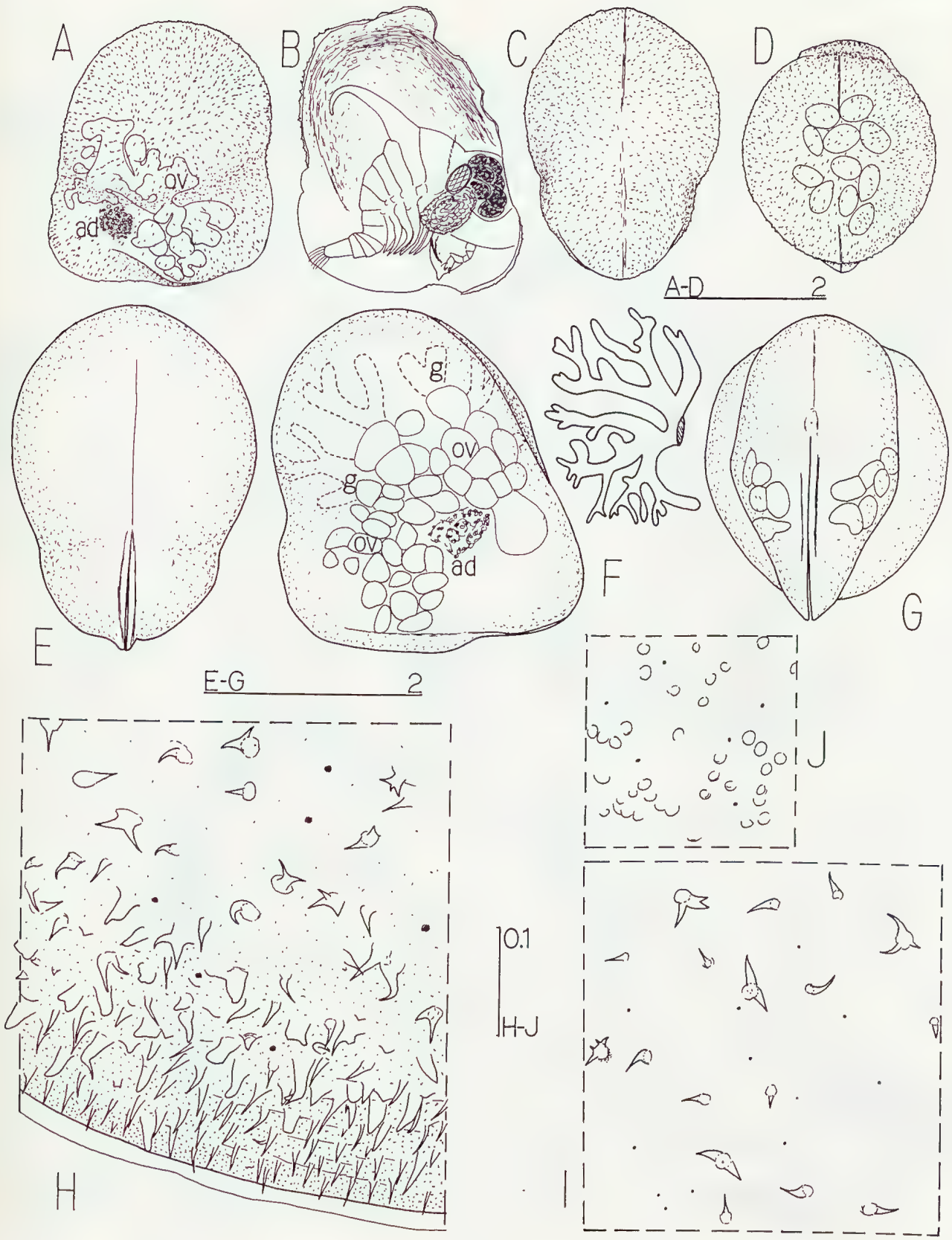


**Fig.3.** *Gorgonolaureus vietnamianus* n.sp. A–D, holotype female (ZIN 1/66583): A, lateral view; B, cutaway to expose main body; C, anterior view; D, dorsal view showing brooded nauplii. E–G, paratype female (ZIN 2/66584): E, rear view; F, lateral view showing organs within carapace and detail of gut diverticulum of opposite side; G, ventral view. H–I, carapace armament of holotype: H, along aperture; I, away from aperture; J, on inner lining. Abbreviations: ad, adductor muscle; g, gut diverticulum; ov, ovary diverticulum. Scale bars in mm.

**Fig.4.** *Gorgonolaureus vietnamianus* n.sp., holotype female (ZIN 1/66583). A, main body with most thoracopodal and furcal setae omitted. B, left antennule, lateral view. C, detail of right antennule, medial view. D–G, mouthparts: D, labrum, rear view with medial languette inside; E, distal part of mandible; F–G, distal parts of maxillules, G twisted to show setal origins along medial edge; H, maxillae. Abbreviations: ad, adductor muscle site; g, gut diverticulum; ov, ovary. Scale bars in mm.

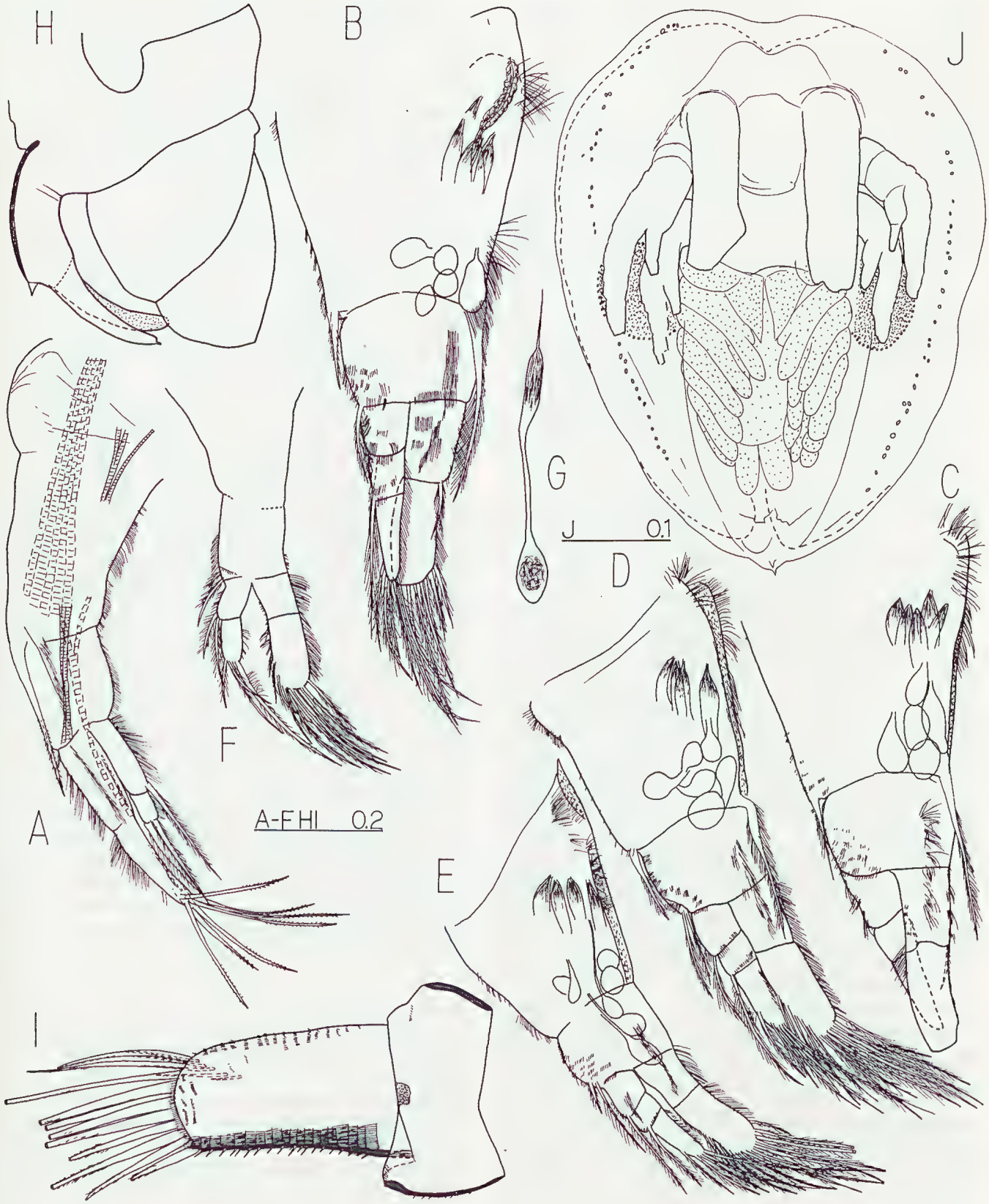


**Fig.5.** *Gorgonolaureus vietnamianus* n.sp. A–I, holotype female (ZIN 1/66583). A–F, left thoracopods I-VI respectively, all in front view except A. G, reconstruction of seminal receptacle (actual appearance shown in B–E). H, first 3 abdominal segments and penis. I, last abdominal segment and furcal ramus in lateral view. J, last-instar nauplius brooded by paratype (ZIN 2/66584) with developing ascothoracid larva (light stippling) and yolk masses (dark stippling) within, setae omitted. Scale bars in mm.

unidentified, uncatalogued paramuriceid gorgonian. E.F. Guryanova, *Pelamida* Stn 29, 27 July 1961, Vietnam, 10°01.6'N 108°35.6'E, 83 m, 34.60‰, 30.19°C, bottom of muddy sand, gravel and broken shells.

**Diagnosis.** Female carapace about 3 mm high, length 85-90% of height, aperture margins simple, external surface wholly covered with claw-like spinules. Gut diverticulum on each side with 3 main dorsal and 3 main ventral branches. Fifth antennular segment longer than sixth and with about 7 setae; proximal sensory process separated from claw guard, aesthetasc reduced to simple seta on latter. Dorsal horn on thoracomere 2 bearing minute spinule rows. Thoracopods reaching to midlength of oral cone. Distal segments of exopods and endopods of pairs II-V with 13-18 setae and 5-6 setae respectively; these limbs containing 5-9 seminal receptacles each, latter varying in diameter along length with round sacs at inner end. Telsonic spines absent; furcal rami broad, subrectangular, with many terminal and a few mediodistal setae.

**Description.** Holotype (Fig.3A-D) 3.3 mm high, 2.8 mm long ventrally, 2.0 mm wide dorsally; respective dimensions of paratype 3.2, 2.8, and 2.2 mm (Fig.3E-G). Carapace univalved, dorsal two thirds consisting of subglobular brood chamber, anterior side somewhat sloping, more so and with medial depression in paratype (Fig.3F). Rear half of somewhat narrower, ventral body chamber evenly tapered (Fig.3G), pair of ventrolateral bolsters in holotype only (Fig.3A). Aperture along posteroventral midline with simple margins, anterior end darkly pigmented; faint seam around most of rest of circumference except dorsally (Fig.3C-E,G). Outer surface covered with spinules and pierced by sparse pores; spinules most dense and diverse along aperture margins (needle-like to very thick and blunt; Fig.3H), with more widely scattered, mostly single and double, claw-like hooks elsewhere (Fig.3I). Delicate inner cuticle with abundant papillae and sparse pores (Fig.3J). Ripe oocytes visible within carapace wall (Fig.3A,F,G); gut diverticula of paratype consisting on each side of dorsal and ventral branch, each immediately dividing into 3, with little successive branching (Fig.3F), those of holotype similar but not clearly seen.

Body of holotype about 2.0 mm long from front of oral cone to tips of furcal rami, that of paratype about 1.8 mm, occupying ventral half of carapace with dorsal horn extending high into brood chamber (Figs 3B, 4A). Cephalic attachment zone vertical, attachment site low on anterior and anterolateral sides of carapace. Head with antennules and oral cone; no eyes or frontal filament complexes found. Extended antennules not reaching tip of oral cone. Adductor muscle tentoria and diverticula of gut and ovary leaving head dorsal to oral cone. Thorax 6-segmented, arched, first segment longest with anterior transverse row of short setae but no filamentary appendages; second segment with long, posteriorly curved horn bearing minute rows of short hairs or cuticular ctenae; sixth with pair of small epaulets. Six pairs of biramous thoracopods gradually decreasing in size posteriorly, tips reaching to midlength of oral cone. Abdomen 5-segmented, third and fourth segments shorter than others. Biramous penis on first segment, pair of furcal rami but no posteroventral spines on telson.

Description of antennules based mostly on holotype (Fig.4B,C). Six-segmented, Z-shaped; first segment short and triangular; second rhomboidal with hairs along part of anterior margin, third triangular with hairs along anterior margin; fourth very short with 2 setae; fifth long and tapered, with 7 anterior setae and some hairs along anterior margin and cuticular ctenae distally near posterior margin; border between third and fourth segments poorly evident in right antennule of holotype, borders between segments 3-5 obscure in paratype. Sixth segment shorter than fifth along anterior margins, narrow at both ends and heavily armed with cuticular ctenae; proximal sensory process at about midlength posteriorly with variably 4-5 setae (3-4 spinulose, apical ones; 1 simple, subapical one); cylindrical, non-flanged claw guard separated from and same size as sensory process, armed apically with 4 short, spinulose setae; weak apical claw with 3 setae anteriorly and to either side of its base.

Oral cone of holotype 0.62 mm long and deep, 0.88 mm wide including pair of lateral bulges (widest part of main body), edges of labrum meeting and joined by interlocking folds behind other mouthparts (Fig.4D). Medial languette 0.39 mm long, linguiform, with rounded tip and dense cover of fine hairs or cuticular ctenae (Fig.4D). Muscular bases of mandibles and maxillules not examined in detail due to damage in dissection; those of maxillules particularly large and occupying bulges in labrum. Distal part of mandible tapering to point (Fig.4E), with tufts of short hairs laterally and unruly short hairs densely placed along proximal two thirds of medial edge. Maxillules (Fig.4F,G) with short hairs at tip, at proximal end of medial side, and submarginally on anterior face; comb row of about 70 longer setae along most of medial margin, with 16 similar setae in groups of 1-6 forming very incomplete second row posterior to them. Maxillae tapered, basally fused, tips bifid with delicate anterior and posterior flanges and movable posterior hooks (Fig.4H).

First thoracopod about 1.7 times longer than sixth, with lateral swelling (genital papilla) at base (Fig.5A). Thoracopods (Fig.5A-F) paddle-like with long, tapered coxa, short rectangular basis (longer than wide in first pair, otherwise wider than long, protopod poorly segmented in sixth pair), 2-segmented exopod with long, equal segments in first pair, shorter ones with distal segment longer than basal in other thoracopods, and 3-segmented endopod (2-segmented in first and last pairs, unsegmented in left thoracopod I of paratype); endopod much shorter than exopod in first thoracopod due to minute proximal segment, in other thoracopods endopod at least three quarters as long as exopod, with first 2 segments together (or first alone in last pair) as long as first exopod segment. Thoracopod I lined with short, fine hairs medially, along lateral edge of exopod, and along medial edge of first exopod segment (Fig.5A).

Thoracopods II-V similarly lined laterally except on basis, with 2 distally converging rows on coxa; medial edges with shorter hairs and cuticular ctenae, latter also covering much of anterior side of medial part of basis and first 2 endopod segments (Fig.5B-E); other hairs fringing lateral side of distal endopod segment and medial side of distal exopod segment. Thoracopods I-V also with anterior field of longer hairs going from lateral part of basis onto first exopod segment. Thoracopod VI lined with fine hairs distal to midlength of basis (Fig.5F). Major setation of left thoracopods of both specimens compiled in Table 3, longest setae about as long as rami, paratype more setose. All setae plumose except for spinulose coxal and exopodal setae of first thoracopod. On endopods II-VI, lateralmost of 3 apical setae longest, but on exopods, longest of apical setae near middle of array, 5 apical setae in holotype, 6-7 in paratype, with no real distinction between apical and medial setae in last pair; usually 1-2 subapical lateral setae on exopods and large number of medial setae.

Seminal receptacles laterally within coxae of thoracopods II-V, about 5-7 per limb in holotype, 7-9 in paratype (Fig.5B-E). Shape not perfectly clear due to surrounding tissue; visible parts including round inner reservoir filled with amorphous substance and narrower, tapered, proximal end filled with longitudinally striated material (presumably sperm) and leading into fine duct surrounded by cord of cells (Fig.5B); proximal and distal parts assumed to be connected by unseen narrow tubes (Fig.5G).

Penis of holotype with short, curved, anteriorly thickened shaft ending in short spine and pair of curved, asetose rami (Fig.5H).

Furcal rami of holotype 0.41 mm long, 0.20 mm high basally, slightly tapered, tip slightly produced (Fig. 5I), those of paratype 0.35 mm long, 0.21 mm high basally and more tapered; lateral face with at least 20 ventral rows of long hairs and some short dorsal ctenae, medial face as seen in paratype largely covered with short ctenae. Holotype with 11 terminal setae on left ramus, longest ones almost as long as ramus, and 5 short, mediodistal setae; paratype with 13 terminal and 4 medial setae on left ramus; distal parts of setae biserially spinulose.

**Nauplii** (Fig.5J). Holotype brooding 112 nauplii (not illustrated) averaging 0.46 mm long, 0.36 mm wide (n = 9), with arrowhead-shaped yolk mass and 2 or maybe 3 unshed exuviae, at earliest stage of development of ascothoracid larva. Paratype brooding 95 late nauplii ready to molt to ascothoracid larva, averaging 0.47 mm long, 0.37 mm wide (n = 14), with 2 loose exuviae and smaller, bilobed yolk mass. More detailed information only available for paratype brood (Fig.5J). Frontal filaments and nauplius eye absent, dorsal pores present but pattern not discerned, equatorial pores present ventrally around rim, labrum very small, minute terminal papilla and bumpy furcal lobes present posteriorly. Antennules unsegmented, armed at a late instar (unclear which one, perhaps last) with 2 short medial setae ('a' and 'b'), small subapical claw rudiment, short subapical lateral seta ('f'), and 2 apical lobes, medial one bearing long and very short setae 'd' and 'e', lateral one bearing 1 very short and at least 1 long 'g' seta. Protopods of antennae and mandibles not clearly observed; exopods at third from last instar with 5 setae on antennae, 4 on mandibles, endopod with 2 apical setae on antennae, perhaps also on mandibles, proximal parts of apparently 2-segmented endopods not seen. Developing ascothoracid larva with short, rounded maxillules, pair of pointed maxillae, 6 pairs of biramous thoracopods, and furcal lobes.

**Remarks.** *Gorgonolaureus vietnamianus* n.sp. is about 50% larger than *G. bikiniensis* and has more highly branched gut diverticula, a relatively smaller sixth segment on the otherwise similar antennule, no long hairs on the thoracic horn, about twice as many setae on the distal segments of the thoracopodal exopods, multiple seminal receptacles instead of two per limb, no telsonic spines, much broader furcal rami with longer setae, and smaller metanauplii. Its overall appearance is somewhat more similar to *G. muzikae*, but the new species is about half as large as that one, with simple rather than interdigitating carapace aperture margins, less complicated gut diverticula, fewer setae on the fifth antennular segment (7 versus 11-12) and lacking two thin extensor muscles of the sixth segment that originate in the fourth segment in *G. muzikae* (cf. Grygier, 1987b), fewer setae on the distal endopod segments of thoracopods II-V (5-6 versus 7-11), differently shaped and fewer seminal receptacles, no posteroventral telsonic spines, and relatively longer furcal rami with slightly fewer setae. Some apparent differences from Grygier's (1981b) original description of *G. muzikae* are due to errors in the latter (Grygier, 1984b): wrong mouth position (before medial languette), missed transverse band of thoracic setae (present on first thoracomere), supposed partial medial fusion of thoracopodal coxae (medial margins simply shorter than lateral ones) – all actually as in *G. vietnamianus* n.sp.

The present nauplii are roughly comparable to those of *G. muzikae* (cf. Grygier, 1987a), though considerably smaller (0.46 mm versus 0.70 mm). However, while the present antennules have a claw rudiment and show more consolidation distally than instar III in *G. muzikae* (namely they are comparable to final instars of several other ascothoracidans; Grygier, 1987a, Grygier, in press, Itô & Grygier, 1990), the exopodal setae of the antennae and mandibles of the third from final instar are as few as in instar I of *G. muzikae*. Perhaps *G. vietnamianus* has only three naupliar instars, while *G. muzikae* is inferred to have at least five (Grygier, 1987a).

The present find is even more shallow, at 83 m, than *G. decurvatus* n.sp. reported above. In 1983 I examined an unidentified, *Gorgonolaureus*-infested, Indonesian gorgonian in the Copenhagen Zoological Museum from a similarly shallow depth, but it could not be located for detailed study a year later. The present host

gorgonian is a paramuriceid, and in older, obsolete classifications it would have been considered to belong to *Placogorgia* (F.M. Bayer, personal communication), but its poor condition and the lack of knowledge of South-east Asian gorgonians in general prevents a true identification.

**Etymology.** Named for the type locality, Vietnam.

### *Gorgonolaureus tricornutus* n.sp.

Figs 6–8, Table 4

**Type material.** HOLOTYPE female (Muséum National d'Histoire Naturelle, Paris, MNHNP Ci2047) with carapace opened and trunk separated from head; 3 PARATYPES (Ci2048): dissected paratype female with brood, dissected male (right furcal ramus and frontal filament complex lost), and undissected specimen, sex uncertain; 2 old, empty cysts. Each specimen occupying separate cyst composed of several polyps on host gorgonian *Eunicella* sp., specimen HGP-46, ORSTOM New Caledonia, N/O *Vauban*, Campagne SMIB 1, Stn DW14, 7 Feb. 1986, 22°58.5'S 167°22.5'E, 640 m.

**Diagnosis.** Adult female carapace almost spherical, length and height equal, about 7 mm, outer surface with posteroventral spinules, giving way to sparse dorsal bumps, aperture margins simple. Naked dorsal horns on thoracomeres 1-3, third one shorter than others. Fourth antennular segment with 2 setae, fifth with about 5, sixth with claw guard only slightly separated from proximal sensory process (also in male). Mandible medially armed with hairs and few small, basal teeth. Maxillae trifid, lacking posterior hooks. Cluster of about 8-15 long seminal receptacles in coxae of thoracopods II-V. Coxa and basis of thoracopods II-IV each with 4-6 medial setae (also in male). Small posteroventral telsonic spines present. Furcal rami 4 times longer than basal width, somewhat tapered, with many short terminal and dorsomedial setae. Male lacking dorsal thoracic horns, fifth antennular segment tapering distally, 12-14 setae on second exopod segment of thoracopods II-V.

**Description of females** (based mostly on paratype) (Figs 6-7). Carapace univalved, that of holotype more or less spherical, 6.9 mm long and high, 6.0 mm wide, with pair of low anteroventral bolsters and laterally compressed posteroventral section bordering aperture (Fig.6A,B). Carapace of paratype female damaged and not measured. Aperture occupying about one sixth of circumference, faint seam visible along rest of midline. In paratype, dorsal brood chamber lined internally by long setae. Single row of widely spaced guard setae on each side posteroventrally just inside aperture. Externally, dorsal part of carapace with sparse bumps, anteroventral region smooth, and posteroventral region densely set with small, slightly curved spinules. Arrangement of internal organs of carapace not determined.

Main body (Fig.6C) attached by oblique attachment zone to anteroventral part of carapace. Body length of paratype 3.3 mm from front of oral cone to tips of furcal rami, height 3.3 mm from tip of oral cone to rear dorsal margin of thoracomere 1. Head with long free dorsal side, antennules, frontal filament complexes, and oral cone; no eyes observed. Thorax 6-segmented, each segment progressively shorter, first segment with anterior fringe of short setae broken at midline and no filamentary appendages, sixth with small lateral epaulets, each segment with pair of biramous thoracopods, their tips falling short of end of oral cone. First 3 thoracomeres each with naked dorsal horn, first two 4-5 mm long and curving backwards, third one short. Abdomen bent 90°, with 5 short, cylindrical segments, third and fourth especially short; small penis on first segment, posteroventral telsonic spines on fifth below blade-like furcal rami.

Antennules 6-segmented, reaching midlength of oral cone when folded, probably reaching tip when extended (Fig.6C,D). First 5 segments tending to become narrower distally: first segment broad, triangular; second parallelogram-shaped with hairs along anterior margin; third segment triangular with dense fringe of longer hairs anteriorly; fourth very short, with short hairs and 2 equal setae on anterior edge; fifth segment with sparse hairs and 5 short setae along anterior edge. Sixth segment about two thirds as long as fifth, broadening distally, with dense cuticular ctenae along margins and thin, movable, distal claw; 3 tiny setae at base of claw; claw guard as long as claw, with 2 setae behind and 1 before apical hood; proximal sensory process about half as long as claw guard, slightly separated from it, bearing 3 short, apical setae and slightly longer, subapical aesthetasc. Musculature of first segment unclear, but rest similar to that of *Gorgonolaureus muzikae* (cf. Grygier, 1987b), except no medial extensor muscles of sixth segment seen to originate in fourth, flexors of sixth segment forming narrow bundle in fifth, and flexor from medial side of third segment inserting on fourth instead of fifth segment.

Frontal filament complex consisting of blunt cone 180 µm long and 90 µm across and somewhat longer, thinner, digitiform piece (Fig.6E); correspondence to parts of homologous organs in other ascothoracidans unclear.

Oral cone triangular, slightly longer than deep in side view. Labrum not examined in detail. Medial languette pointed, trough along anterior edge lined on both sides by short hairs, posterior edge with fine distal hairs (Fig.6F). Mandible (Fig.6G,H) broad and flat basally with 3 muscles, distal part rapidly tapering to needle-like, minutely bifid or undivided tip; lateral edge with indentation and row of hairs, proximal ones longer; medial edge with dense, imprecisely arranged fine hairs flanked on each side submarginally by shorter cuticular ctenae; basal part of medial edge with few apically dissected teeth, also some simple spines on

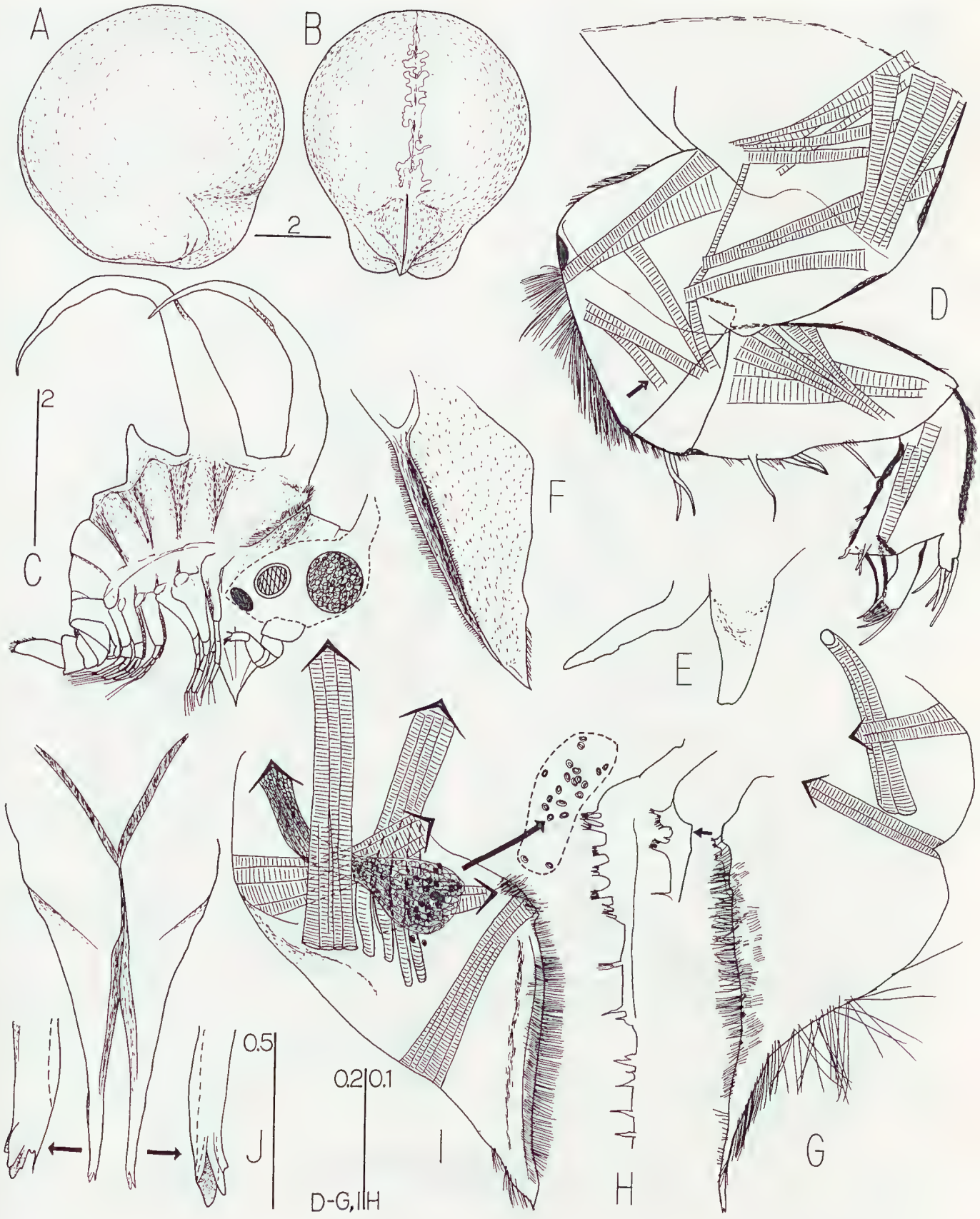


**Fig.6.** *Gorgonolaureus tricornutus* n.sp., females. A–B, lateral and rear views of holotype (MNHNP Ci2047). C–J, paratype (Ci2048): C, main body; D, left antennule, lateral view, aberrantly placed muscle marked by arrow; E, frontal filament complex; F, medial languette; G, left mandible with detail of base; H, detail of base of right mandible, fine hairs omitted; I, right maxillule with detail of pores; J, maxillae with details of tips. Scale bars in mm.

right mandible of paratype. Maxillule (Fig.6I) broad basally but less flattened than mandible due to extensive musculature, distal part evenly tapered and shorter than that of mandible; lateral edge with few distal hairs; medial edge with patch of fine hairs at base, and comb-row of about 175 setae flanked on one side by row of spinules, on other side by more or less orderly arrays of short, fine hairs, and, farther from edge, by row of laterally directed hairs; basal part of latter side also bearing field of about 20 pores associated with nervous ganglion. Maxillae fused basally, stylet-like distal parts with trifid tips, apical structures neither hook-like nor movable (Fig.6J).

Thoracopods in form of tapered, biramous paddles, second pair longest, first pair a little shorter with weak segmentation, remainder decreasing in length posteriorly, last pair only two thirds as long as second (Fig.7A-E). Coxa making up half of length; basis shorter

**Fig.7.** *Gorgonolaureus tricornutus* n.sp., paratype female (MNHNP Ci2048). A–E, left thoracopods I, II, IV, V, and VI, respectively, A and B in rear view, others in front view, seminal receptacles shown diagrammatically in B–D. F, lateral body wall at bases of thoracopods II (right) and III (left), showing seminal receptacle duct papillae (y). G, penis. H, left furcal ramus, lateral view. Scale bars in mm.

than wide; 2-segmented exopods slightly longer than endopods in thoracopods II-VI, endopods 3-segmented (2-segmented in thoracopod VI), exopod much longer than weakly 2-segmented endopod in thoracopod I. First thoracopod with large genital papilla at base (Fig.7A), bearing ventral bump and minute dorsal process (filamentary appendage?). Edges of thoracopods extensively lined with fringes of fine hairs. In thoracopods II-V (Fig.7F), row of hairs along both edges of narrow, triangular, lateral face of coxa; posterobasal part of coxa produced into round lobe, anterobasal part sclerotised as condyle for limb promotion and remotion; extrinsic muscles inserting on both lateral corners of coxa; posterior notch between condyle and pleural lobe containing oval swelling with openings of seminal receptacles, and deep, triangular depression. Major thoracopodal setae all plumose except on first pair, length half to two thirds that of rami. Left thoracopodal setation of paratype compiled in Table 4. On first thoracopod, usual lateral coxal seta shifted onto proximal quarter of basis. Distal exopod segments of thoracopods III-V with 3 apical setae and 2 subapical lateral setae (thoracopod VI with 4 and 1 setae, respectively), remaining setae medial.

Cluster of cylindrical seminal receptacles within proximolateral part of coxa of thoracopods II-V (Fig.7B-D), their number unclear, at least 6-8, maybe 15 or more per thoracopod. Illustrated musculature (Fig.7A,B,E) comparable to that of *G. muzikae* (cf. Grygier, 1984b, 1987b).

Penis stubby, slightly curved, with small, anterodistal spine and pair of short, stubby rami with several minute setae (Fig.7G). Telsonic spines very small, about 55 µm long, fully fused with telson, upper side hairy. Furcal rami (Fig.7H) about 0.63 mm long, twice as long as basal height, tapering distally and slightly downturned, right ramus with 24 short, spinulose setae extending along distal margin (6 setae), distal part of dorsal margin, and dorsal part of medial face; marginal and submarginal cuticular ctenae also present.

**Description of male paratype** (Fig.8). Carapace bivalved, 3.4 mm long, 2.6 mm high, 1.7 mm wide (Fig.8A,B). Lateral outline parallelogram-shaped with slightly convex anterior and ventral edges, fusiform in dorsal view. with broader anterior end. Valves separate except along dorsal hinge line, and exhibiting small anterior gape, posteroventral part exposed outside of host cyst. External surface smooth but with many pores, inner side of at least posteroventral margin bearing guard setae. Sperm-filled testes forming loop with about 6 posteriorly or ventrally directed, subdividing side branches.

Body somewhat shrivelled, with head, 6-segmented thorax apparently lacking dorsal horns and filamentary appendages, and 5-segmented abdomen. Abdominal segments 2 and 5 square in side view, equally long; segments 3 and 4 triangular, with short dorsum. All expected appendages present.

Antennule like that of female in most respects (Fig.8C), but relatively larger, about same length as oral cone when folded, segments 2, 5, and 6 somewhat longer relative to their widths, 2 setae on segment 4 unequal, about 10 long setae on fifth segment, and sixth segment longer relative to fifth due to extended distal half. Claw very slender with nearly straight portion at midlength, claw guard with lateral flange, almost all setae on this segment (also aesthetasc) relatively much longer than in female.

Frontal filament complex consisting of 2 long, slender, plumose parts (Fig.8D), ventral one 1.1 mm long and plumose to base, posterior one 1.6 mm long, only distal half plumose. No basal appendix observed on ventral part, but thick proximal aesthetasc present, shorter than filaments of plume (latter 300-550 µm long).

Oral cone 0.74 mm long, 0.44 mm deep, sharp spout comprising one quarter of length (not illustrated). Labrum surrounding other mouthparts, latter not dissected, exposed tips of maxillae bifid with small posterior hooks.

Six pairs of biramous, paddle-like thoracopods lacking seminal receptacles (Fig.8E-G). Thoracopodal segmentation as in female, including very short, poorly biarticulate endopod of first thoracopod; other endopods only a bit shorter than exopods. Thoracopods extensively fringed with fine hairs, but not on lateral side of basis. Setae of terminal segments of rami much longer than in female, about two thirds as long as rest of limb, but lateral and medial setae much shorter than these. All major setae plumose, except setules much shorter on first thoracopod. Setation very similar to that of female (Table 4), including numbers of apical and lateral setae on distal exopod segments.

Penis (Fig.8H) with long shaft slightly shorter than thoracopodal protopods, with double row of small, lateral setae and thickened anterior edge ending in small spine; pair of vermiform rami half as long as shaft, each with about 6 short, thin, distal setae. Posteroventral telsonic spines small and dorsally hairy (Fig.8I). Furcal rami as long as abdominal segments 4 and 5 combined, 0.69 mm long, one quarter that high at base, slightly tapered to truncate and slightly downturned end (Fig.8J). Closely set row of 22 long, medial setae up to 1.0 mm long (most proximal ones much shorter), 5 distal setae of varying lengths (longest 0.58 mm, ventral one shortest); all setae plumose and contributing to tail fan. Cuticular ctenae distally along dorsal margin and along most of ventral margin.

**Eggs.** Paratype brooding more than 215 subspherical eggs, many lost or crushed, major axis of eggs averaging 0.50 mm (n = 18).

**Remarks.** The assignment of *G. tricornutus* n.sp. to *Gorgonolaureus* is tentative. The presence of several dorsal horns suggests that this species ought to be assigned to either *Isidascus* Moyse or *Cardomanica* Lowry (cf. Moyse, 1983; Grygier, 1984; Lowry, 1985), but in those genera the three or four horns are on thoracomeres 2 to 4 or 2 to 5, while the present females have them on thoracomeres 1 to 3. Both of these other

**Fig.8.** *Gorgonolaureus tricornutus* n.sp., paratype male (MNHNP Ci2048). A, dorsal view. B, lateral view showing branched testes. C, right antennule, medial view. D, frontal filament complex. E–G, right thoracopods I, III, and VI, respectively. H, penis. I, posteroventral telsonic spine. J, right furcal ramus, lateral view, only bases of some setae shown. Scale bars in mm.

genera also have very long filamentary appendages associated with the first thoracopods, as well as more than one comb row of setae on the maxillules and prominent proximal teeth medially on the mandibles, and they have many more medial coxal setae on thoracopods II to IV; *Isidascus* has a uniramous penis in both sexes. Other species of *Gorgonolaureus* agree with *G. tricornutus* in lacking filamentary appendages, having only one maxillular comb-row, lacking mandibular teeth (details of mouthparts are unknown in the type species, however), and having a biramous penis (as does *Cardomanica*). *Isidascus* has a delicate outer cuticle except near the aperture and inhabits calcareous galls on an isidid gorgonian, and *Cardomanica* lives attached (usually by characteristic outgrowths of the carapace) to chrysogorgiid gorgonians, and may not always be covered by host tissue (Lowry, 1985; Grygier, 1990b), whereas the new species, like other species of *Gorgonolaureus*, is encapsulated by a number of host polyps.

Within *Gorgonolaureus*, the new species is most similar to *G. muzikae* in terms of size, appendage armament, and seminal receptacles (see Grygier, 1981b, 1987d). The principal differences in the females, besides the extra dorsal horns, are the more spherical carapace with simple rather than interlocking aperture margins, fewer setae on the fifth antennular segment, some basal teeth on the mandible, twice as many setae medially on the coxae of thoracopods II to IV (same distinction also valid in the males), and considerably longer furcal rami. The male also differs from those of *G. muzikae* ("protanders" of Grygier, 1981b) in lacking a dorsal horn, having a tapered sixth antennular segment with the claw guard and proximal sensory process only slightly separated, and in having fewer setae on the second exopod segment of thoracopods II-IV. The eggs are larger than those of other species parasitising gorgonians.

The host, *Eunicella* sp., has usually been classified in the Plexauridae, a family also said by Bayer (1981) to include the paramuriceid hosts of other species of *Gorgonolaureus*. However, Bayer (1981) transfered this genus to the Gorgoniidae, which makes *G. tricornutus* the first ascothoracidan parasite from that family of gorgonians.

**Etymology.** From the Latin *tri-* meaning three, and *cornu* meaning horn, referring to the three thoracic horns.

### *Flatsia* n.gen.

**Type species.** *Flatsia walcoochorum* n.sp., by monotypy.

**Diagnosis.** Female carapace rounded, bivalved, with brood chamber in each valve and pore plates on concave ventral side. Cephalic attachment zone vertical, anterior. Setose, medial humps on thoracomeres 2-6, epaulets small. Antennules 6-segmented, proximal segments much bigger than distal ones, 1 strong and many weak setae on fourth segment; several short setae on fifth. Sixth segment much shorter than fifth; claw guard short with 4 setae, proximal sensory process directly behind it, bearing 3 setae and aesthetasc. Labrum with long, straight tip. Medial languette present. Mandibles with lateral setae, medial teeth, and toothed, needle-like tip. Maxillules with 2 medial setal combs. Maxillae bifid with posterior hooks. Conical filamentary appendage extending anteriorly from base of thoracopod I; heavily setose, laterodistal knob on coxa of that limb. Protopod of thoracopod VI undivided; thoracopodal endopods and exopods equal in length, endopods 3-segmented in thoracopods II-IV, 2-segmented in thoracopods I and V, undivided in thoracopod VI, exopods 2-segmented except undivided in thoracopod VI. Thoracopodal setae about as long as rami, lateral coxal seta often absent on thoracopods II-V, distal segments of endopods and exopods of these limbs with similar numbers of seta, seta found occasionally on medial corner of first exopod segment. Many elongate seminal receptacles in thoracopods II-V. Abdomen 5-segmented; first segment with biramous, setose penis; fifth with pair of telsonic spines and elongate, tapered, hairy furcal rami with many short, ventral setae and 2 apical ones. Host unknown. This detailed diagnosis may require changes if additional species are discovered.

**Etymology.** Named for Murray Ball's comic strip "Footrot Flats" ("Fæhunden" in Danish), which I greatly enjoyed while studying ascothoracidans for 16 months in Denmark and Australia. Gender feminine.

### *Flatsia walcoochorum* n.sp.

Figs 9–11, Table 5

**Type material.** HOLOTYPE female with 295 brooded nauplii (AM P37803, vial and 6 slides of dissected appendages), J.C. Yaldwyn & D.J. McMichael, 22-23 June 1963, off Port Stephens, NSW, 73-82 m, muddy bottom. Host uncertain. Specimen found loose in vial with small, apparently normal actinian; pennatulacean from same haul also showing no obvious signs of infestation.

**Diagnosis.** As for genus.

**Description of holotype.** Carapace dull orange in preserved state, bivalved, 5.74 mm long, 5.57 mm high, 4.26 mm wide (Fig.9A-D). Rounded in side view except for shallow ventral indentation, oval in vertical view with anterior end more rounded. Ventral side with teardrop-shaped, slightly concave surface 3.7 mm long, 2.5 mm wide and spindle-shaped gap between valves exposing oral cone and anterior thoracopods. Valve edges free from mid-dorsum to anteroventral corner and distinct seam clearly visible on all but lowest part of

**Fig.9.** *Flatsia walcoochorum* n.gen. n.sp., holotype female (AM P37803). A–D, lateral, ventral, dorsal, and posterior views, respectively, A with dotted outline of organs within carapace. E, ornamentation of ventral surface of carapace (between arrows), lateral side above, medial side below, with detail of one pore-plate. F, left half of carapace removed, exposing main body and brood. G, left antennule, lateral view, with details of setal armament of segments 4-6. Scale bars in mm.

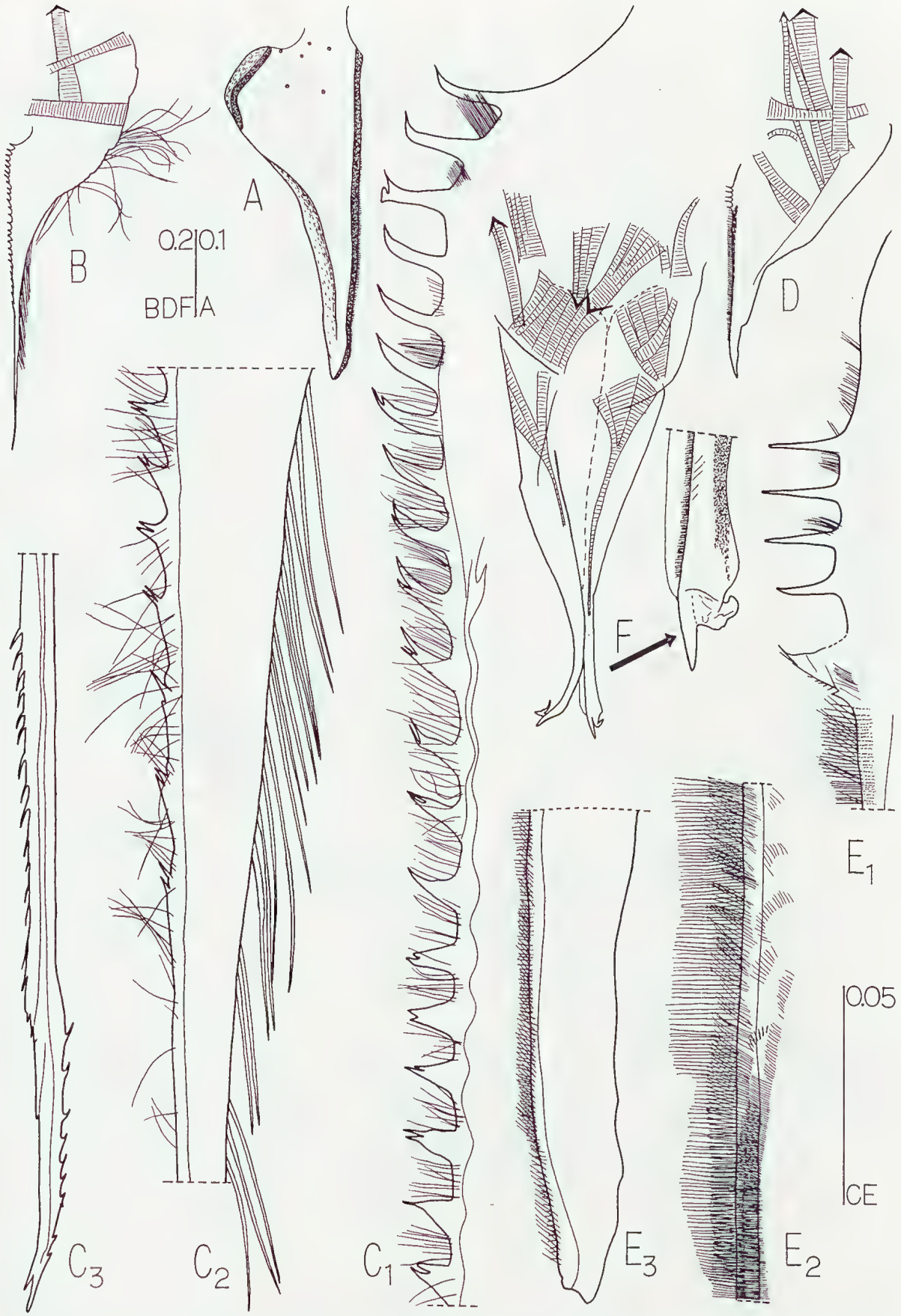


**Fig.10.** *Flatsia walcoochorum* n.gen. n.sp., holotype female (AM P37803), mouthparts. A, medial languette. B, left mandible and $C_{1-3}$, successively more distal details of its distal part. D, left maxillule and $E_{1-3}$, successively more distal details of its medial edge, submarginal short comb-row on far side omitted in $E_2$. F, maxillae with detail of tip. Scale bars in mm.

anterior side. Dorsal valve margins produced into low, narrow flanges, less pronounced anteriorly and posteriorly. Brood chamber anterodorsally in each valve, inner submarginal parts of valves flat and closely appressed (Fig.9F). Most of external surface dotted with pores and short setae, and inner surface with scattered pores, but valve margin more complicated, especially ventrally (Fig.9E): band of dense, fine hairs just submarginally on medial face; concave ventral surface with denser setae than elsewhere and with round or oval, possible slightly convex 'pore-plates' with up to 40 oval-rimmed, slit-like pores each, fewer pores per plate towards edges of this region. Internal organs of carapace (gut and ovary diverticula) with 3 main, subdivided branches, anterior, dorsal and posterior (Fig.9A).

Main body about 4.4 mm long and high, excluding thoracopodal setae (Fig.9F). Head attached to carapace anteriorly, bearing antennules and oral cone, and giving off gut and ovary diverticula and adductor muscle tentorium on each side; no eyes or frontal filaments seen. Thorax 6-segmented, arched, segments equally long and high except for laterally compressed, triangular or quadrangular humps on segments 2-6, last 2 of these pointing anterodorsally. Humps fringed with short, sparse setae, most abundant on thoracomere 6. Sixth segment also with pair of small lateral epaulets. Six pairs of biramous, paddle-like thoracopods, first pair accompanied by filamentary appendages at base. Abdomen small compared to thorax, J-shaped, third and fifth segments about as long as high, others shorter. First segment with short, biramous penis and few short, dorsal setae; fifth segment with medium-long pair of posteroventral spines situated side-by-side and pair of long, tapered furcal rami.

Antennules (Fig.9G) 6-segmented, somewhat prehensile, basal part massive, segments becoming much smaller distally. First segment right triangular, deeper than long, with scattered pores on lateral face and tuft of long, posterodistal hairs. Parallelogram-shaped second segment largest, about one third as deep as long. Third segment triangular, as long as deep, with hairs along anterior edge and anterior part of lateral face, distal hairs shorter and sturdier. Fourth segment very short, anterior edge with 1 strong seta laterally, about 15 weaker ones with frayed tips medially. Fifth segment quadrilateral, slightly curved and tapered, with about 9 short, setulate setae along middle part of anterior margin. Sixth segment about one third as large as fifth, with convex posterior margin and strong, retractable, distal claw with short seta to each side (anterior margin obscured, expected seta there unconfirmed); fixed claw guard just behind and about half as long as claw, with lateral flange, 2 medium-long and 2 short, distal setae and apical hood; proximal sensory process immediately behind claw guard with aesthetasc and 3 distal setae, all of same length. Antennular musculature generalised (cf. Grygier, 1987b), except only 1 claw retractor muscle, no thin extensor muscles connecting medial side of fourth segment to base of sixth, and no dorso-anterolateral muscle in segment 2.

Labrum forming conical sheath, posterior margins joined behind maxillae but not fused; straight, slender tip unusually long (Fig.9F). Languette 0.38 mm long, sharply pointed with several lateral pores at base (Fig.10A), straight anterior edge lined with extremely short, dense hairs, posterior surface trough-like. Mandible (Fig.10B,$C_{1-3}$) 0.94 mm long, basal width about 0.25 mm, 3 muscles in base, hairs along its lateral edge becoming shorter distally. Attenuated process making up two thirds of length of mandible, basal two thirds of medial edge with about 30 evenly spaced, slightly curved, simple or bifid teeth, distal ones shorter, with numerous interspersed fine setae; tip needle-like with distally pointing spinules along medial edge, retrorse spinules on lateral edge. Maxillules (Fig.10D,$E_{1-3}$) similar in form to mandibles, but distal part shorter and less attenuate, base more muscular; outer face with longitudinal trough for mandible, straight medial edge with 5 basal teeth and 2 combs of marginal and submarginal setae running along whole length and becoming shorter distally, accompanied by some submarginal ctenae on each side. Maxillae (Fig.10F) fused to level of midlength of languette, basal part massive with transverse grooves for muscle attachment, distal parts 0.8 mm long, becoming very slender, tips bifid with diaphanous flange and movable posterior hooks.

Thoracopods I-IV about 1.6 mm long without setae, measured along medial edge, thoracopod V about three quarters as long, thoracopod VI about one-half (Fig.11A,C-G). Protopods with relatively broad, distally tapering coxa and small, narrow basis longer than wide (protopod undivided in thoracopod VI). Exopods 2-segmented (undivided in thoracopod VI), first segment shortest. Endopod 2-segmented in thoracopods I, V, and VI (distal segment longer), and 3-segmented in thoracopods II-IV (second segment short, distal one longest). Rami equally long except endopod half as long as exopod in thoracopod VI. Lateral margins of thoracopods (only coxa in thoracopod I) typically profusely hirsute, medial part of coxa with rows of short hairs (but profuse long hairs on thoracopod I and distally on protopod in thoracopod VI), lateral edge of endopod and medial edge of first exopod segment also lined with hairs in thoracopods II-VI. Anteriorly directed, 1.0 mm long, conical filamentary appendage at base of thoracopod I (Fig.11B), this limb also with laterodistal coxal knob bearing many distally hirsute setae, one of them trifid (Fig.11A). Setal counts of left thoracopods given in Table 5. Thoracopodal setae typically about as long as rami, plumose except setules very short in thoracopod I. Highly unusual occurrence of medial seta on first exopod segment in thoracopods III and IV (Fig.11D,E). Coxae of thoracopods II-V containing laterobasal cluster of flask-like, long-necked seminal receptacles opening on dorsolateral swelling at base of limb (Fig.11D). In one case (thoracopod II), seta seen on lateral body wall above this swelling. Number of seminal receptacles estimated at 19 in thoracopod II,

**Fig.11.** *Flatsia walcoochorum* n.gen. n.sp., holotype female (AM P37803). A–G, left thoracopods, all except D in rear view: A, thoracopod I, omitting most of coxa (twisted) and with details of exopodal setal armament and B, of filamentary appendage; C, rami of thoracopod II, showing only bases of setae; D–E, thoracopods III and IV, respectively, with seminal receptacles shown in D (also present in thoracopods II, IV, V); F, rami of thoracopod V, showing only bases of setae; G, thoracopod VI with detail of exopodal setal armament (setal bases only shown). H, penis. I, left furcal ramus, medial view. Scale bars in mm.

at least 10 in thoracopod III, over 8 in thoracopods IV, 12 in thoracopod V. Penis (Fig.11H) about 0.6 mm long, shaft with curved anterior edge and about 12 short, thick, posterior setae, distal part short, posteriorly flexed, bearing 2 short, cylindrical rami with 8-9 short, slender setae each.

Furcal rami elongate (Fig.11I), 1.42 mm long, 0.34 mm high at base, 0.06 mm high at tip. Dorsal edge straight, unarmed; ventral edge slightly concave and rising, with abundant, spine-like setae; lateral and medial faces covered with short, thin hairs; 2 distal setae, dorsal one twice as long.

**Nauplii** (not illustrated). Typical brooded ascothoracidan nauplii (see Grygier, 1987a). Oval in dorsal view, averaging 0.48 mm long (n = 17), about 1.3 times longer than wide, more rounded in front than rear, yolk occupying rear half of body. Labrum small, ill-defined; 3 pairs of naupliar limbs and blunt terminal spine (small furcal lobes seen in minority of specimens). Antennule with long and short subterminal setae, medium and very long terminal setae; status of medial setae unclear. Antenna with probably unarmed protopod, weakly annulate exopod with 5 setae, and unsegmented endopod with tiny medial spine at midlength, subterminal seta, and apical spine and 2 apical setae. Mandible like antenna, but with only 4 setae on exopod.

**Remarks.** It is difficult to assign *Flatsia* n.gen. with certainty to any of the families recognised by Grygier (1987c). It is clearly advanced compared to the ectoparasitic, bivalved synagogids *Synagoga* Norman and *Waginella* Grygier, and it seems to have its greatest morphological affinities with the gorgonian-parasitising synagogid genera *Gorgonolaureus*, *Cardomanica*, *Isidascus*, and *Thalassomembracis* (see Grygier, 1981a, 1981b, 1984a; Moyse, 1983; Lowry, 1985).

The carapace is intermediate between the low, fully bivalved one of *Waginella metacrinicola* (Okada, 1926) and the ovoid one of *Cardomanica*, which is functionally univalved but still has a long, dorsally extending aperture. The ventral pore plates are unique to *F. walcoochorum* n.gen. n.sp., and they suggest that some kind of secretion is produced, perhaps for attachment to the unknown host like the cement pads of *Waginella* spp. living on crinoids (Grygier, 1983). The mid-dorsal humps on the thorax are reminiscent of those in several species *Thalassomembracis*, which, however, have transverse rows of setae, not longitudinal ones as here (Grygier, 1984a). The only other ascothoracidan with similar humps is the ctenosculid *Endaster hamatosculum* Grygier (1985c). The multiple thoracic horns in other ctenosculids, *Cardomanica*, and the dendrogastrid *Ulophysema*, which might be regarded as modifications of these humps, do not involve more than four segments, and never the sixth.

Six-segmented antennules are plesiomorphic in the Ascothoracida. The enlarged basal segments here are similar to those of females in various echinoderm-infesting genera of the order Dendrogastrida, but then in 4- or 5-segmented antennules; the pores on the first segment are unique. Possession of one instead of two strong setae on the fourth segment is typical of most species of *Thalassomembracis*; the similarity of that seta to its accompanying ones is unusual. Possession of an adjoining claw guard and proximal sensory process, both with the maximum setal armament, is typical of females of gorgonian-infesting genera (except *Thalassomembracis*), although these genera often have only three setae on the claw guard, not four.

Such a long labral tip is unique to *Flatsia*. The mandibular armament resembles that of *Synagoga*, but with a much finer distal process and the teeth more widely spaced (cf. Norman, 1913; Grygier, 1983). The maxillular armament, with two rows of setae, is typical of *Thalassomembracis*. The filamentary appendages resemble those of *Isidascus* and *Cardomanica*, but similar ones also occur in several diverse dendrogastridan species.

A two-segmented endopod in thoracopod V occurs very sporadically in the Synagogidae. No synagogid has more than a single lateral coxal seta on thoracopod I, and all of them do have such a seta on thoracopods II to IV but usually not on V and VI, the opposite of the present case. The number of major medial setae (positions 6–9) on thoracopods II to IV is higher than any synagogid, but is approached by females of *Cardomanica* and *Isidascus*. The relatively high number of terminal exopod setae (position 4) on the first thoracopod compared to other limbs is held in common with *Cardomanica*, *Synagoga mira* Norman, and the metacrinine crinoid-infesting species of *Waginella*. Such closeness in the setal counts of each limb's exopod and endopod is only approached by the same two species of *Waginella*, where the exopod usually has just two to three more setae than the endopod (Grygier,1983). Occasional possession of a medial seta on the first exopod segment is unique to *Flatsia*. The seminal receptacles are like those of *Gorgonolaureus muzikae* and *Cardomanica* spp. in form and number. The small, biramous penis is usual for females of *Gorgonolaureus*, while in related genera it is reduced to a uniramous nub. It is unusual for the telsonic spines not to be widely separated. The furcal rami are unlike those of other genera in detail.

All this suggests that *Flatsia* n.gen. might best be classified as an aberrant representative or perhaps the sister-group of the gorgonian-infesting group of genera within the Synagogidae. It has no clear synapomorphies with, for example, the higher families in the order Laurida, the Lauridae and Petrarcidae.

**Etymology.** Named for Wallace ("Wal") Footrot and Cooch Windgrass, protagonists of "Footrot Flats."

**Lauridae** Gruvel, 1905

***Baccalaureus*** Broch, 1929

***Baccalaureus isauricola* n.sp.**

Figs 12, 13

**Type material.** HOLOTYPE female (AM P37808), 3 PARATYPE males (AM P37809) removed from single polyp of zoanthid *Isaurus tuberculatus* (AM G15233) [specimen mentioned by Muirhead & Ryland (1985)], R.A. Birtles & P.W. Arnold, 26 Mar. 1979, Great Barrier Reef off Townsville, Qld, Australia, James Cook Univ. Benthic Research Unit Square 6A, Stn 442, 18°48'S 146°55'E, 36 m. Holotype and largest paratype dissected; cephalic appendages of former and some thoracopods of latter lost in dissection.

**Diagnosis.** Female carapace oval in side view, lateral coils making 1.5 revolutions, medial face of coiled lobe armed with bispinose papillae. Thoracic horns short, straight, naked. First thoracopod short, filamentary appendage small; thoracopods V and VI absent; thoracopods II-IV with few distal setae, unsegmented but with short, seminal receptacle-free, distal part, about 10-12 seminal receptacles per thoracopod. Thoracic tergites separated by expanses of arthrodial membrane, no dorsal setae on thorax or abdomen. Furcal rami with 3-4 terminal setae and numerous dorsal or dorsomedial setae. Male lacking anteroventral pits on carapace, nauplius eye present, antennular claw denticulate, lobe-like penis short and setose, furcal rami with 3 terminal setae.

**Relation to host.** Female located within base of polyp, surrounded by thin coat of host tissue and with carapace aperture protruding through small hole in polyp wall. Polyp tissue firmly adhering to female aperture, and males partly embedded in polyp wall material externally (Fig.12A,B).

**Description of female** (Fig.12). Carapace oval in side view, 7.8 mm high, about 5.3 mm wide, 4.8 mm long without apertural protrusion, lateral lobes of carapace coiled, making just over 1.5 turns (Fig.12A-C). Coil edges and, to lesser extent, exposed faces finely wrinkled. Medial face of each lobe with arcuate field of papillae, each papilla bearing paired, opposed spines spanning 25 µm (mean of 16) (Fig.12D,E). Aperture protrusion just above midheight, 1.4 mm long. Aperture fringed with fine setae, margins separated posteriorly, joined but separable ventrally, with 3 sets of attached arcs of exuvial cuticle (Fig.12F).

Body 3.0 mm long from tip of thoracic horns to tips of furcal rami (Fig.12F,G). Most of head lost; large adductor muscle tentoria present. Thorax 6-segmented, thoracopods I-IV present. Anterior thoracic horns straight, naked, about 1.3 mm long along ventral edge, directed anteroventrally and tapering to rounded tips. Thoracic tergites 2-6 separated by long expanses of arthrodial membrane. Lateral chitinous ridge apparently formed of adjoining, thickened, ventral edges of tergites 2-4 and sinuous anterior extension reaching onto lateral part of horn base; ventral edges of tergites 5 and 6 thickened only at front and rear, so not part of chitinous ridge. Abdomen 4-segmented, bent 90° at triangular third segment. No dorsal setae on any thoracic or abdominal segments. First abdominal segment with penis, last with furcal rami.

Only right thoracopods examined in detail. Thoracopod I short, lobe-like with distal seta (Fig.12H); oval, basal swelling (filamentary appendage) 0.42 mm long, 0.35 mm wide when flattened, extending short distance over chitinous ridge (Fig.12G). Thoracopods II-IV long, uniramous, unsegmented (Fig.12I-K), tapering to point with uncertain but small number of setae in thoracopod II, 2 setae in thoracopod III, 1 apical and a few lateral setae in thoracopod IV. Seminal receptacles filling thoracopods II-IV except for short distal region, 9-12 elongate sacs with long, thin ducts seen per limb, emptying on prominent lateral papilla at limb base.

Penis vestigial, not reaching midlength of second abdominal segment. Furcal rami tapered (Fig.12L,M), 0.28 mm long along dorsal edge, 0.13 mm high at base, about one quarter as high distally, dorsal and ventral margins spinose, 3 hirsute distal setae on left ramus, 4 on right, 10 setae about half as long as distal one arising medially along distal half of left ramus (1 on dorsal margin, others inclined dorsally), 11 on right ramus, including many more on dorsal margin.

**Description of male** (based on largest paratype) (Fig.13). Elliptical in dorsal view (Fig.13A); in lateral view dorsum straight, posterodorsal margin oblique, rest of margin curved, possibly with very slight posteroventral scalloping (Fig.13B).Three specimens 0.51, 0.52, 0.57 mm long, smaller ones 0.34 and 0.37 mm wide, respectively, height slightly less than width. Weak external polygonal meshwork of chitinous ridges (Fig.13C), complete meshes about 14 µm across; scattered setae and pores at equal densities; no anteroventral pits. Large accumulations of sperm within valves. Body (Fig.13D) divided into head with large antennules compared to oral cone, short, 6-segmented thorax with 6 pairs of thoracopods, and 4-segmented abdomen bent sharply at third segment. Large, red nauplius eye within medial protrusion of 'forehead' anterior to labrum (Fig.13D,E). First 4 thoracomeres short and equal, last 2 elongated dorsally. Abdomen with penis on first segment, furcal rami and telsonic spines on last. Body length and height of dissected specimen 0.30 mm from front of oral cone to tips of furcal rami and from tip of oral cone to top of thorax.

Antennules 6-segmented, Z-shaped (Fig.13D), first bend occurring at triangular third and short fourth segments, latter with 2 short, equal setae on anterior margin. Fifth segment longest, with 2 unequal setae near base. Sixth segment oblong with movable, spinulose claw; frontal and lateral seta (at least) at base of claw; laterally flanged claw guard with 2 long distal setae and damaged tip

**Fig.12.** *Baccalaureus isauricola* n.sp., holotype female (AM P37808). A–C, lateral, rear, and front views of carapace, respectively, host tissue adhering to aperture in A and B, males indicated by arrows in B. D, right half of carapace, medial view, spinose areas stippled and E, enlarged. F, situation of body within carapace. G, body (head lost). H–K, right thoracopod I and left thoracopods II-IV, respectively, latter three showing seminal receptacles, and lining of duct shown for one in I. L–M, right and left furcal rami, respectively, in lateral and medial view. Scale bars in mm.

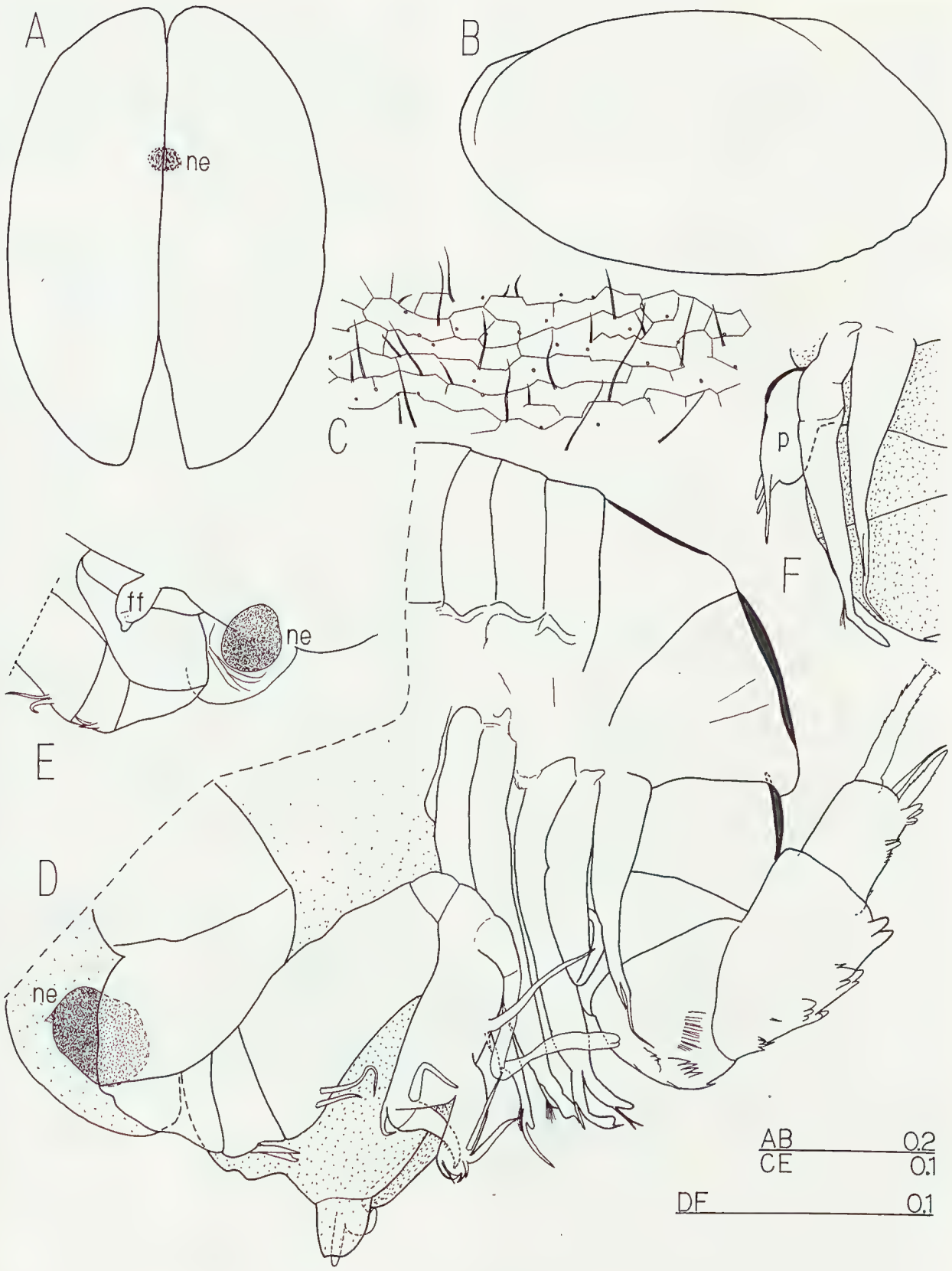


**Fig.13.** *Bacclaureus isauricola* n.sp., paratype male (AM P37809). A–B, dorsal and lateral views, respectively, showing nauplius eye (ne). C, external ornamentation of middle of lateral side. D, main body. E, "forehead" region seen from right side, with frontal filament (ff). F, penis (p) and last two left thoracopods. Scale bars in mm.

apparently bearing 2 setae behind and one in front of apical hood; long seta and short spine (latter only seen in right antennule) arising midway between claw guard and long, proximal aesthetasc, latter with bifid tip on left antennule. Small frontal filament seen lateral to base of right antennule (Fig.13E). Oral cone not dissected; labrum apparently with anterior crest and maxillae bifid with posterior hooks (Fig.13D).

All thoracopods long and slender (Fig.13D,F), but fifth and sixth successively shorter than rest, sixth half as long as first. Left thoracopods I-V: I with apical seta and short lobe, and subapical tuft of hairs; II biramous, endopod with tuft of hairs, exopod with minute seta; III hidden in this preparation; IV biramous, exopod with minute seta, endopod with 2 minute terminal setae; V uniramous with subapical tuft of hairs. Left and right thoracopods VI uniramous with subapical seta. Right thoracopod V biramous, endopod filiform with hairs, exopod half as long, with 2 tiny setae.

Penis very short with 3 unequal distal setae (Fig.13F). Third abdominal segment with ventral cuticular ctenae, some spiniform (Fig.13D); fourth segment with pair of basal ctenae, 2 sets of 2-3 blunt spines at half and three quarters length, and pair of short, blunt telsonic spines. Furcal rami rectangular, about 1.5 times as long as high, with 2 clusters of blunt, ventral spines at two thirds of length and terminally (Fig.13D); 3 terminal setae, dorsal one twice as long as others and spinulose, middle one simple and thin, ventral one intermediate in thickness, spinulose.

**Remarks.** The female of *Baccalaureus isauricola* n.sp. has many features that are unique or nearly so in the genus. Such a high oval carapace is only approached by *B. torrensis* among the species with coiled brood sacs, but there the aperture protrusion is much more dorsal (cf. Pyefinch, 1937). The bifid spines on the carapace are a new feature, other species having only simple papillae, or sometimes large papillae or simple spines; the present spines are smaller and simpler than the rosette papillae found in confamilial *Laura* spp. (cf. Grygier, 1985a). The clear division of the thorax into short tergites and large areas of arthrodial membrane is only otherwise known in a different laurid genus, *Zoanthoecus* (cf. Grygier, 1985a), but it is also evident by SEM (not light microscopy) in *Baccalaurus falsiramus* Itô & Grygier, 1990. Such short thoracic horns are only found in *B. verrucosus* Pyefinch (1939), where they are hairy, and in the new Japanese species, where they are naked but sometimes have upturned tips. The number of thoracopods can be variable within a species in this genus (Itô & Grygier, 1990; Grygier, unpublished data); this aside, *B. hexapus* Pyefinch (1936) is the only other species to lack thoracopods V and VI, but it has long, coiled thoracic horns and reportedly a peculiar sort of first thoracopod. In the new species, the furcal rami are relatively much shorter and also much more heavily armed with mediodorsal setae than any other in the genus, where there are at most a few small medial setae or sensilla. All the other species of *Baccalaureus* have dorsal setae at least on the last thoracomere and first abdominal segment, and most often on other segments as well. It is unfortunate that the antennules and mouthparts remain undescribed, but antennular morphology is known to be variable within a species (Itô & Grygier, 1990), and the mouthparts are essentially alike throughout the Lauridae (Grygier, 1985a; Grygier, 1990b; unpublished data). Even without the cephalic appendages, the present female has enough distinctive features to allow recognition in the future and separation from other species now.

In the Lauridae, males of *Baccalaureus japonicus* Broch (Yosii, 1931; Okada, 1938) and of two species of *Zoanthoecus* (Grygier, 1985a; Grygier, 1990b) have been well described. The present males are like *B. japonicus* in lacking anteroventral carapace pits, and in having a network-like ornamentation of the carapace. A possible male of *Baccalaureus falsiramus* also has cuticular reticulation (Itô & Grygier, 1990). Such reticulation is different from the spinule arrays covering males of *Zoanthoecus*, but is similar to, though less developed, than the reticulation on so-called Tessmann's larvae, as least one form of which is known to be the ascothoracid larva of *Baccalaureus* (Grygier, 1988b; Itô & Grygier, 1990). The antennules, thoracopods and abdomen are not substantially different from those of the other males, but the male of *B. isauricola* n.sp. is the only one with a spinulose antennular claw (as in Tessmann's larvae), its thoracopod VI is much better developed than in *B. japonicus*, and the three terminal setae on the furcal rami agree in number and form with *B. japonicus*, but not with the *Zoanthoecus* species, which have four. The anomalously high total of five setae on the claw guard, four being the normal maximum, may be an observational error in the present case. The other males have extremely long, uniramous penes, sometimes with a few minute distal setae. None of them have a nauplius eye; in fact, the present males represent the first record of adult ascothoracidans with a nauplius eye.

The only previously known Australian species of *Baccalaureus* is *B. torrensis* from *Palythoa howesi* at Thursday Island, Torres Straits (Pyefinch, 1937). *Baccalaureus isauricola* n.sp. is the first species of the Lauridae known to infest *Isaurus*, a genus of zoanthids with three currently recognised species (Muirhead & Ryland, 1985). *Isaurus tuberculatus*, the present host, is pantropical, so its ascothoracidan parasite may also be widely distributed.

**Etymology.** Named for the host genus, *Isaurus* and Latin *icola* (inhabitant).

### *Baccalaureus cannoni* n.sp.

Figs 14, 15

**Type material.** HOLOTYPE female (AM P37807), CSIRO Cr. 0183, Stn B4S, 15 Feb. 1983, off WA, 19°5.3-5.1'S 118°54.0-53.4'E, 83 m; PARATYPE female (Queensland Museum W12661), QFS sample AQSIB/97,

north-east Qld, 16°46.0'S 146°3.8'E, 40 m; PARATYPE female and exuvia found within its carapace (Zoological Institute, Leningrad, ZIN 1/66585), NPS *Knipovich*, Stn 613, trawl 456, 12 Mar. 1966, Andaman Sea, 9°31.8'N 97°35.3'E, 83-86 m; PARATYPE female (Queensland Museum W12662), slightly damaged at aperture, L. Cannon, May 1973, Moreton Bay, Qld. First 3 specimens dissected, ZIN specimen brooding some eggs and harbouring a hyperparasitic, cryptoniscus-stage, cryptoniscid isopod.

**Diagnosis.** Female carapace oblong, with body chamber at one end and lateral brood chambers as

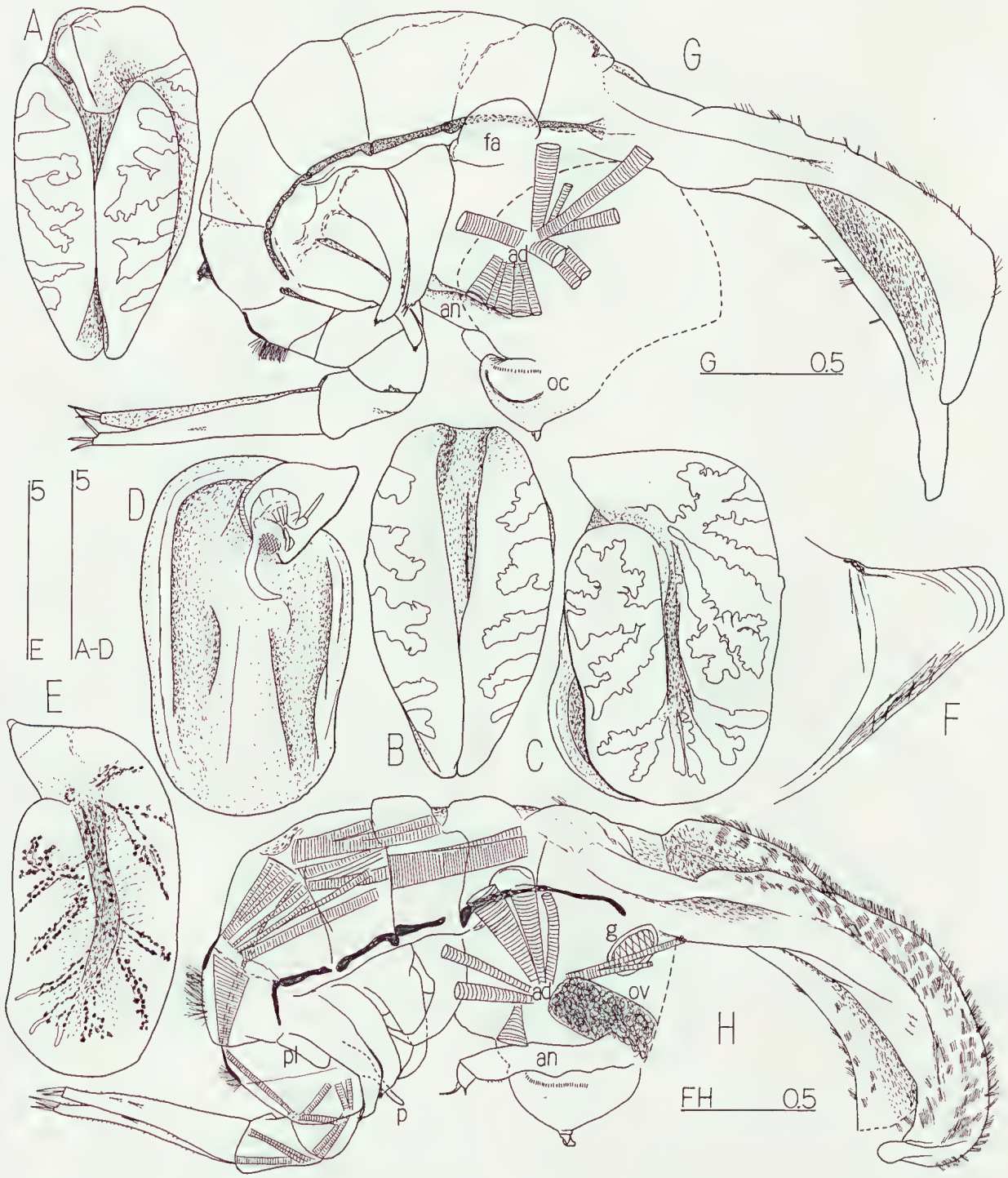


**Fig.14.** *Baccalaureus cannoni* n.sp., females. A–D, holotype (AM P37807): A–C, rear, front, and lateral views, respectively; D, left half of carapace removed to show situation of main body; E–F, paratype (ZIN 1/66585): E, lateral view; F, medial view of aperture protrusion. G–H, main bodies of holotype and ZIN paratype, respectively. Abbreviations: ad, adductor muscle; an, antennule; fa, filamentary appendage; g, gut diverticulum; oc, oral cone; ov, ovary; p, penis; pl, transverse plate. Scale bars in mm.

**Fig.15.** *Baccalaureus cannoni* n.sp., females. A, right and distal part of left antennules of ZIN paratype exuvia; B, antennules of W12661 (Qld). C, mandible (md) and distal part of maxillule (mx) of W12661; D, tips of one maxilla each of W12661 (right) and ZIN paratype exuvia (left), arrows pointing to ventral process. E, left (upper) and right (lower) filamentary appendage of holotype, with vestigial thoracopod I next to former; F, right thoracopod I and filamentary appendage of W128661. G–I, thoracopods of ZIN paratype; G, right thoracopods II-V and transverse plate (pl), showing seminal receptacles and ducts; H, distal parts of left thoracopods II, III, and V, showing tissue strands to seminal receptacles in last; I, tips of several thoracopods of exuvia. J,K, furcal rami of holotype and ZIN paratype exuvia, respectively. Scale bars in mm.

uncoiled, simple sacs 1.5-2 times longer than deep, each with lateral longitudinal furrow and 2 medial longitudinal furrows. Thoracic horns about as long as body proper, curving about 90°. Oral cone with row of spine-like striations internally on each side. Thoracopod I short or absent, with relatively small, oval, filamentary appendage at base. Thoracopods II-V usually vaguely 2-segmented, proximal portion of each largely filled with up to 40 or more seminal receptacles. No sixth thoracopods, but broad, apron-like, ventral lobe present on that segment. Dorsal setae on last (sometimes also second to last) thoracomere and first abdominal segment. Penis reaching end of second abdominal segment. Furcal rami straight, with 2-3 terminal and a few medial setae, cuticular ctenae weak and mostly limited to medial surface.

**Host.** All specimens were infesting *Sphenopus marsupialis* Steenstrup, large, solitary zoanthids from soft bottoms. First 3 specimens attached to inner wall of hosts' gastrovascular cavities, but uncertain whether host body wall penetrated by carapace aperture; last specimen previously removed from host. All parasites with thin, adhering layer of pink host tissue over the entire surface except aperture. One of 18 examined zoanthids from Moreton Bay infested, 1 of 37 from various Western Australian localities.

**Description.** Carapace with triangular body chamber and pair of elongate, anteroventrally extending brood sacs U-shaped in side view due to longitudinal furrow (Fig.14A-C,E). Holotype 9.5 mm long, 5.1 mm wide, 5.8 mm deep (from front to rear of brood sacs), W12661 6.8 *x* 4.7 *x* 3.6 mm, ZIN specimen 9.78 *x* 5.97 *x* 4.84 mm, W12662 11.38 mm long, 4.23 mm wide. Front and rear edges of each brood sac folded medially, forming 2 additional broad furrows on medial side (Fig.14D). Body chamber extending slightly beyond rear margin of brood sacs, slit-like aperture running from just dorsal of tip along entire ventral side; tip densely lined with hairs internally, possible growth bands visible externally, but no adhering arcs of exuvial cuticle (Fig.14F). Body chamber connected to lumina of brood sacs by anterolateral openings through which thoracic horns reach (Fig.14D). Outer cuticle thin, most delicate on medial faces of brood sacs, tougher near aperture, externally papillose except near aperture. Diverticula of gut and ovaries in each brood sac consisting of simple longitudinal branch along medial side and ramifying lateral branch along floor of lateral furrow (Fig.14C,E).

Main body of holotype 3.2 mm long from front edge of horns to tips of furcal rami, 1.4 mm high from tip of oral cone to top of thorax (Fig.15G). Body of W12661 4.4 *x* 2.2 mm (along same axes), that of ZIN specimen (Fig.14H) 3.4 *x* 1.5 mm, and 0.77 mm wide at thoracomere 4. Attachment zone of head to carapace slightly inverted, thorax extending somewhat anteriorly over head. Head bearing antennules and oral cone.

Thorax 6-segmented with pair of curved anterior horns on first segment and 4-5 pairs of uniramous thoracopods, sixth pair absent. Thoracic horns about 1.8 mm long in holotype, about 2.3 mm long in W12661, and 2.0 mm in ZIN specimen, length relative to body variable but making up half of body length in holotype (Fig.14G,H). Horns curved smoothly downward and outward about 90°, covered with tufts of thin, basally directed hairs, most abundant on proximodorsal margin. Rear of thorax bent downward, dorsal setae on last 2 thoracomeres in W12661 (shorter on segment 5) but only on sixth thoracomere in holotype and ZIN specimen. Ventrolateral edge of each thoracic tergite formed into thickened rod articulating with those of adjacent segments, together forming lateral chitinous ridge extending anteriorly onto base of horn.

Abdomen 4-segmented with sharp posterior bend at third segment. In W12661, boundary between first 2 segments unclear on right side and segment 4 partially divided dorsally; in ZIN specimen, first 2 segments poorly distinguished on both sides (Fig.14H), but clear in exuvia (second segment triangular, with extremely short dorsum and extensive arthrodial membrane). First 3 segments with cuticular ctenae and lateral pores, latter most abundant on first segment. Dorsal setae and posteroventral penis on first segment, furcal rami on fourth.

Antennules extending posteriorly from each side of base of oral cone, about equal in length to longest thoracopods and to furcal rami (Fig.14H). Segmentation usually obscure, possibly 4 segments in holotype, but distinct distal segment apparent in both antennules of ZIN specimen (Fig.15A). Apical spine and aesthetasc, latter on short process, in holotype and ZIN specimen, just aesthetasc on process in W12661 (Fig.15B). Cuticular ctenae present, especially dense on distal half.

Mouthparts based almost entirely on W12661, except ZIN exuvia useful for labrum. Labrum markedly deeper than long, laterally bulbous. Rear margins adjoining behind maxillae for short distance, terminal aperture with short spout. Basoposterior inner cuticle of labrum seeming to be produced into row of strong spines with about 8 setae between successive spines; however, this structure apparently actually a chitinous skirt with spiniform stays, perhaps involved in junction between labrum and bases of mouthparts. Mandibles narrow, with oblique medial edge bearing short, retrorse hairs (Fig.15C); maxillules with slightly longer and wider, blunt tips than mandibles and with broad, muscular bases. Maxillae massive, distal third of length free, tips bifid, anterior point bigger than posterior, latter not hook-like (Fig.15D).

In holotype, first right thoracopod short and stubby, left one absent (Fig.15E), both sides with oval swelling (filamentary appendage) reaching slightly dorsal of lateral chitinous ridge (Fig.14G). Short first thoracopods, each with a seta, and filamentary appendages also present in W12661 (Fig.15F), but only filamentary appendages found in ZIN specimen. Thoracopods II-V (Fig.15G-I) about equally long, uniramous, usually unsegmented, but with distinctly narrower distal region (latter lacking on right

thoracopod V of W12661); tiny but distinct apical segment seen on left thoracopod III and right thoracopod V of ZIN specimen. Distal part armed with fine hairs and ctenae and 3-9 short, apical setae (also 2 subapical setae on right thoracopod V of ZIN specimen). Proximal parts of thoracopods largely filled with seminal receptacles, minimum of 21, 51, 42, and 30 counted in right thoracopods II-V of W12661, appearing grouped into 2 clusters in most thoracopods in that individual, large but undetermined number also in thoracopods II-V of holotype and ZIN specimen (Fig.15G), but not in exuvia of latter. Fine, cell-lined ducts of seminal receptacles opening basolaterally with no distinct papilla; inner ends of receptacles attached to cuticle by tissue strands (Fig.15H). Thoracopods VI absent, but transverse ventral plate with square corners present instead in all specimens (Fig.15G).

Penis unarmed, uniramous (?absent in exuvia), little longer than ventral side of second abdominal segment, tip nozzle-like in W12661, long and narrow in ZIN specimen (Fig.15G).

Furcal rami straight and evenly tapered, 0.8 mm long in holotype, 1.0 mm in W12661, 0.70 mm in ZIN specimen, length 4.3-5.5 times basal height (furcal rami of ZIN exuvia only 0.33 mm long and 3.7 times longer than high). In holotype, right ramus with 3 apical setae, left with 2, dorsalmost seta slightly longer on both, 1 spine-like medial seta on each ramus; W12661 with 3 apical setae on each ramus, dorsal seta longest, 2 medial setae on left ramus, 3 on right (Fig.15J); ZIN specimen with terminal setation as in holotype (also in exuvia; Fig.15K) and 1-2 medial setae per ramus. Short cuticular ctenae covering medial surface, much weaker or absent on lateral face (only near ventral edge in exuvia).

**Remarks.** This new species is assigned to *Baccalaureus* despite several peculiarities because: it has a pair of lateral brood sacs unlike the other laurid genera; these sacs are not very different from those of the type species, *B. japonicus* Broch; a pair of thoracic horns is present (also found in one species of *Laura* Lacaze-Duthiers; Grygier, 1985a); there are continuous transverse bands of setae on some of the abdominal and rear thoracic segments (a newly recognised generic characteristic contradicted only by *B. isauricola* n.sp.); and the furcal rami are elongate (distinguishing it from *Laura*).

No other described species of *Baccalaureus* has a terminal body chamber; usually it is at about midheight posteriorly. A young specimen of *B. pyefinchi* Brattström illustrated by Pyefinch (1939: fig.1, as *B. japonicus*) is the most similar to the present form in this regard. Most species of this genus have coiled brood sacs; the least coiling until now, a slight posterior bend of the ventral parts, is exhibited by *B. japonicus*. Its brood sacs are simple, like those of *B. cannoni* n.sp., but they lack longitudinal furrows, and the body chamber is at midheight posteriorly. The short, hirsute, downturned thoracic horns of the new species are most similar to those of *B. verrucosus* Pyefinch (1939), where they are even shorter. All other species except *B. isauricola* n.sp. and *B. falsiramus* (see Itô & Grygier, 1990), in which the horns are short, naked, and straight or upturned, have very long, downwardly coiled horns. Variability in antennular morphology has been documented before by Itô & Grygier (1990). The mouthparts are poorly known in most other species of *Baccalaureus*, but the present ones are similar to those of other laurids (Grygier, 1985a; Itô & Grygier, 1990). The striated structure resembling a row of teeth or spines in the labrum has not been described before. No other described species of *Baccalaureus* has seminal receptacles in thoracopod V, although they are found there in most ascothoracidans, including some other laurids (Grygier, 1985a).

This is the first record of an ascothoracidan parasitising zoanthids of the monotypic genus *Sphenopus*. There is very little literature on this genus, and the only significant report on its biology (Nagabhushanam & Jothinayagam, 1982), which included a study of food and feeding, did not mention any parasites.

The wide geographic range of the present material (eastern and western Australia, Andaman Sea) is unusual in this genus, since most other species of *Baccalaureus* have been reliably reported only from their type locality. It is interesting that the species of *Baccalaureus* that parasitise *Sphenopus* (*B. cannoni* n.sp.), *Isaurus* (*B. isauricola* n.sp.), *Parazoanthus* (*B. japonicus*), and *Zoanthus* (*B. falsiramus*) are very distinct from each other and from the five described species infesting *Palythoa*. The latter are quite similar to each other except principally in thoracopod development, which is not a reliable specific character. Perhaps too many *Palythoa*-infesting species have been recognised. I am currently studying the variability within large populations of *Baccalaureus* in an attempt to answer this question.

**Etymology.** Named in honour of Dr Lester Cannon, Queensland Museum, who first discovered the species and brought it to my attention.

**Petrarcidae** Gruvel, 1905

**Petrarcinae** Gruvel, 1905

***Petrarca*** Fowler, 1889

***Petrarca okadai*** Grygier, 1981

Fig.16

*Petrarca okadai* Grygier, 1981a: 183–189, figs 1–3; Grygier, 1985b: 1031–1033, fig.2.

**Material examined.** Eight specimens out of 20 in lot (AM P37801): 2 pairs, 1 trio, 1 singleton; from internal galls (*sensu* Zibrowius & Grygier, 1985) in

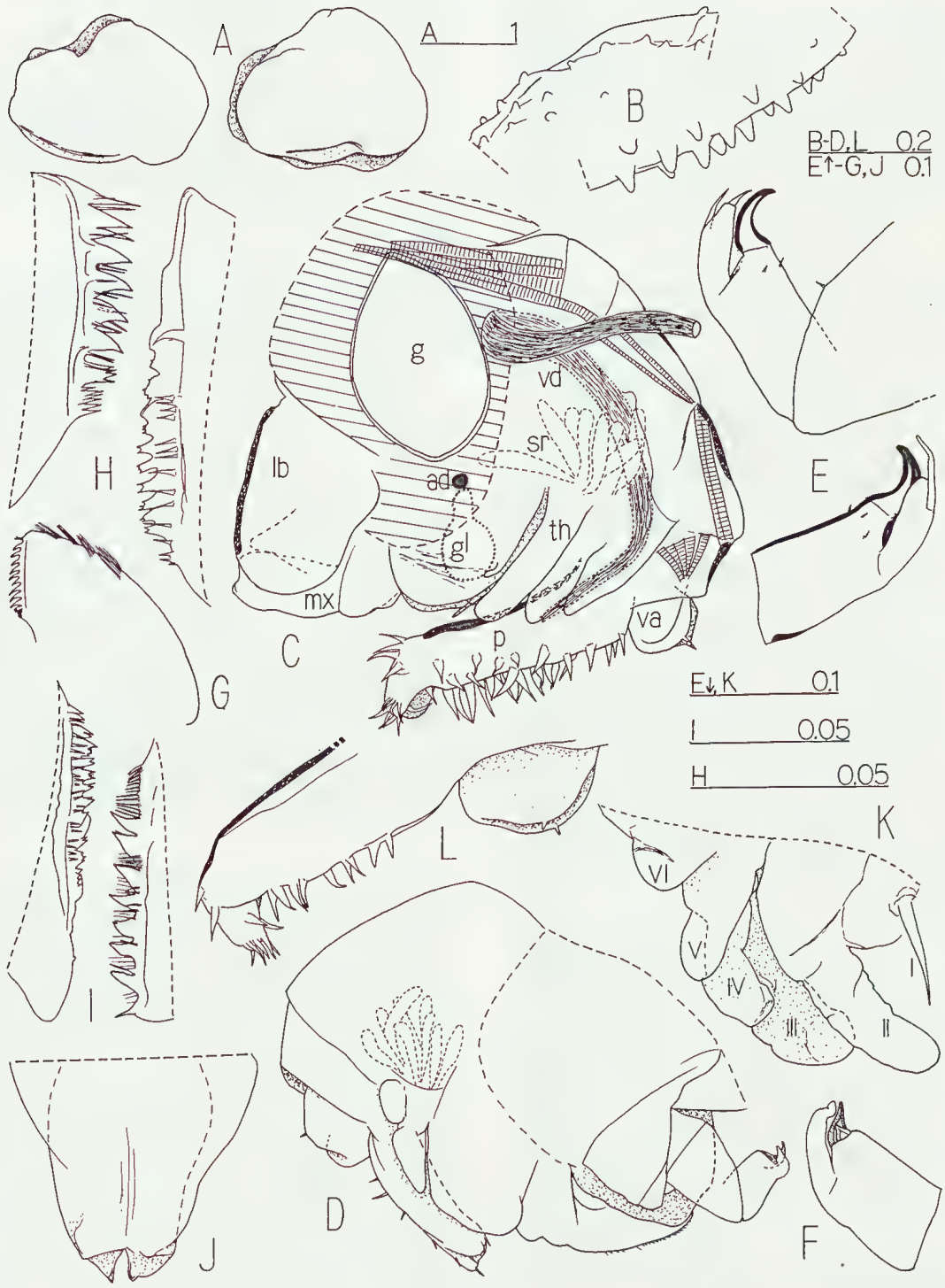


**Fig.16.** *Petrarca okadai* Grygier. A,B,D–I,K–L, Lizard Island, Qld (AM P37801); C,J, Straits of Macassar (MNHNP Ci2148). A, larger pair, lateral view, front ends left. B, posterodorsal (above) and anteroventral (below) carapace valve margins of left specimen in A. C, body removed from carapace, showing some internal organs and dorsal trunk musculature, antennules removed. D, body of aberrant specimen, anterior end right. E, distal segments of two typical antennules. F, double claw and abnormal claw guard on left antennule of specimen in D. G, mandible. H, medial edges of mandible (left) and maxillule (right) of one member of trio. I, medial edges of mandible (right) and maxillule (left) from two members of smaller pair. J, maxillae, frontal view. K, full set of thoracopods (cf. C–D). L, abdominal parts of left specimen in A. Abbreviations: ad, adductor muscle; g, gut diverticulum; gl, maxillary gland; lb, labrum; mx, maxillae; p, penis; sr, seminal receptacles; th, thoracopods; va, vestigial posterior abdomen; vd, vas deferens. Scale bars in mm.

*Heteropsammia cochlea* (AM G15229 and P37802), above commensal sipunculid burrows and mostly undetectable externally, J.K. Lowry & R. Springthorpe, 11 Feb. 1987, off Mrs Watson's Beach, Lizard Island, Qld, 12 m. Trio (MNHNP Ci2148) from internal gall in *Heteropsammia* sp., ORSTOM, Campagne CORINDON 2, Stn 293, 10 Nov. 1980, Straits of Macassar, 2°37.74'S 117°49.41'E, 45 m, gall visible externally as lump on one side of columella and extending towards neighbouring septa (Zibrowius, personal communication).

**Morphological variability.** Larger Lizard Island pair 2.0-2.1 mm long, with papillae over whole carapace surface and short but distinct ventral flanges, anteroventral papillae about 3 times longer than others (Fig.16A,B). Macassar specimens 1.3-1.5 mm long, similarly ornamented and with nubbly ventral flanges. Lizard Island trio 1.0-1.2 mm long, with few small to moderate anteroventral papillae on carapace, one specimen also with few tiny papillae along ventral valve margins; submarginal groove present in 2 specimens but no produced flanges. Singleton 1.4 mm long, with almost no papillae and no flanges.

Vestigial seta present on anterodistal corner of fourth antennular segment in some smaller specimens; up to 3 vestigial setae at base of claw, 1 marginal and 1 to each side (Fig.16E). Claw guard usually with 1-2 small, apical spines and with aesthetasc arising between midlength and beginning of distal third. Aesthetasc not accompanied by spinule and either not reaching end of claw guard or exceeding it, maximum length equal to that of claw-facing edge of claw guard. Both claw guards deformed in Lizard Island singleton, and one of its antennules bearing double claw (Fig.16F).

Lateral edge of mandible with several tufts of fine hairs (Fig.16G). Medial edge (Fig.16H,I), starting proximally, armed with 4-14 thin hairs, 6-10 strong, slightly curved teeth, most proximal tooth and sometimes another often bifid or otherwise apically split, and 1-2 more slender distal teeth. Typically 10-20 relatively strong hairs amongst teeth and along one side of tooth row, similar hairs or abundant, finer ones on other side. Medial armament of maxillules restricted to proximal half or two thirds (Fig.16H,I), consisting of thin lamella divided into about 10 weak, distally bifid or multidentate teeth flanked submarginally on one side by irregular row of 10-20 hairlike spinules. Maxillae completely fused into trapezoidal labium, end produced into 4 very short lobes representing ancestral bifid tips (Fig.16J).

Thorax with up to 2 dorsal thickenings in rear half, Macassar specimen and large Lizard Island specimen with 2 transverse dorsal wrinkles more anteriorly (Fig.16C). Pair of setiform first thoracopods of variable length observed in most examined specimens (not in Lizard Island singleton), but number of lobe-like thoracopods as seen in whole mounts of bodies apparently varying from 2-5 per side (Fig.16C,D,K), differing even on two sides of same specimen (lowest on left side of Lizard Island singleton). Cylindrical seminal receptacles within thorax, 5-10 on each side apparently principally associated with second thoracopods, i.e., first lobelike pair (Fig.16C,D).

Penis (Fig.16C,D,L) usually with 10-25 ventral setae along whole length or on distal two thirds of shaft (only 5 setae in Lizard Island singleton), and 7-14 smaller, thinner setae on each small, trapezoidal ramus (rami very weakly developed in Lizard Island singleton). Posterior, vestigial part of abdomen not exhibiting more than 2 segments; its armament, when visible, consisting of 2 spines (Fig.16C,L).

**Remarks.** My earlier concept of *Petrarca okadai* (see Grygier, 1981a, 1985b) included a carapace entirely covered with simple papillae and a thorax with 6 pairs of thoracopods, but according to the present observations, neither feature is actually true for all specimens. The variability recorded in the present specimens from Lizard Island, the type locality for *P. okadai*, in carapace morphology and armament, occurrence and size of antennular armament elements, number of thoracopods (although observations of the last are sometimes difficult in whole mounts), and penis setation provide a warning against giving such features much weight in diagnosing species of *Petrarca*. The most reliable discriminatory features seem to be gross aspects of the carapace armament and details of the mandibles and maxillules, the mouthparts perhaps being best. The singleton from Lizard Island differs most widely from the other specimens, but its bizarre distal antennular morphology allows us to recognise it as aberrant rather than a distinct species.

**Demography of Lizard Island population.** Of 358 *Heteropsammia* collected at Lizard Island as detailed above and split with a hammer and chisel, 14 were currently infested with *Petrarca okadai* and two had empty gall cavities (overall infestation 4.5%). Fisk (1981) previously reported only 0.5% infestation of *H. cochlea* by this parasite at Lizard Island. Of the 14 sets of parasites, two pairs and one set crushed by the chisel were brooding eggs. There were three apparent singletons, two of them notably small, and six pairs without brooded eggs. Two of these pairs were in separate galls in a single host; one other 'pair' may actually have been two singletons in separate galls, but this is quite uncertain. The number of individuals comprising three sets left *in situ* is unclear, but one of them was clearly at least a pair. There were no confirmed trios, and no singletons, with eggs. Two cases of cohabitation of *P. okadai* with the burrowing bivalve *Lithophaga lessepsiana* Vaillant were observed, one involving an empty gall with a tiny hole opening into the inner end of a bivalve burrow, the other involving one of the sets left *in situ*, with a tiny bivalve sitting within a slit at the sipunculid burrow aperture. Large and small bivalves or empty burrows occurred in 39 of 358 corals (10.9%), so the odds of finding even one such cohabitation in the present population are only $0.045 \times 0.109 = 0.0049$ (i.e., p less than 0.01). Two such occurrences in this sample may indicate a tendency for the ascothoracidans and bivalves to co-occur.

### *Petrarca sensoria* n.sp.

Fig.17

**Type material.** HOLOTYPE (AM P37804) and 2 PARATYPES (AM P37805) occupying large internal gall (*sensu* Zibrowius & Grygier, 1985) of columella of undescribed species of *Fungiacyathus* G.O. Sars (determined by S.D. Cairns), another PARATYPE (AM P37806) occurring alone in small internal gall of columella of another specimen from same lot (AM G15230; also including 4 uninfested corals), W.F. Ponder, RANS *Kimbla* Stn 1, 29 Mar. 1969, off Moreton Bay, Qld, 27°31'S 153°40'E, 77-80.5 m. Holotype and singleton paratype dissected, latter referred to as "paratype" in description. Each gall evident as raised, spongy-appearing lump on columella.

**Diagnosis.** Carapace generally smooth and without distinct ventral flanges on valves; large, blunt papillae along middle half of ventral margins, small papillae elsewhere below midheight. Thorax not externally segmented, abdomen with pair of posterior spines. Distal aesthetasc on antennular claw guard about as long as claw guard itself. First pair of thoracopods setiform, others lobe-like, sixth pair extremely reduced. Penis relatively short and thick, rami broad, rounded and heavily setose. Mandible with 8-10 recurved teeth with row of spines on outer face alongside. Maxillule with about 9 delicate teeth, distal ones rounded, basal ones subdivided, row of tiny spinules on outer face alongside.

**Description.** Holotype 1.56 mm long, 1.36 mm wide, 1.28 mm high, its accompanying paratypes 1.30 *x* 1.20 *x* 1.03 mm (front end damaged) and 1.15 *x* 1.03 *x* 0.97 mm; singleton paratype 1.08 *x* 1.01 *x* 0.95 mm. Carapace bivalved but lacking distinct hinge, spheroidal with greatest girth well below midheight (Fig.17A,B); valves thick, completely enclosing main body. Brood chamber absent, one specimen with several spherical eggs 0.16-0.17 mm in diameter adhering to rear of carapace. Middle portion of ventral valve edge with large, blunt papillae, more in holotype than paratype (Fig.17C); similar but more widely spaced papillae dorsal and anterodorsal to these, and small, isolated papillae over entire ventral half of carapace in holotype, but rare in paratype. .

Head comprising half of compact body (Fig.17D), with anterodorsal attachment zone, large, folding antennules, and oral cone. Thorax unsegmented externally, but in holotype, posterior segment indicated by dorsal cuticular thickening and musculature. Six pairs of thoracopods. Abdomen with large first segment bearing enormous, distally bifid penis; vestigial posterior part of abdomen consisting of perhaps 2 segments and bearing pair of small spines on projecting lobes, left spine in holotype much bigger than right (Fig.17K), both equally small in paratype.

Antennules large, strongly developed, 5-segmented (Fig.17E,F). First segment triangular with long base, heavily sclerotised but with much arthrodial membrane around partly recessed second segment, latter quadrilateral with thickened, transverse chitinous band mediobasally and much arthrodial membrane posterodistally. Third segment triangular, asymmetrical. Quadrilateral fourth segment also asymmetrical, longer posteriorly than anteriorly, with tiny seta at midpoint of short anterior margin in paratype. Fifth segment almost rectangular, distal edge bearing heavy, movable claw and trough-like claw guard. No more than 2 tiny, variably placed sensilla seen at base of claw, up to 2 more sensilla seen at tip of claw guard. Long, thin, subapical aesthetasc about as long as claw guard proper in holotype, slightly longer in paratype. Spinule at base of aesthetasc in 3 of 4 cases.

Labrum relatively large with pair of posterolateral flaps flanking maxillae, main part containing pharyngeal pump muscles. Mandibles and maxillules both with rounded lateral margin and short, toothed, medial edge, maxillules slightly broader. Toothed edge of mandible 87 µm in holotype, 53 µm in paratype; left one of holotype (Fig.17G) with 10 teeth, distal 8 simple and recurved, basal 2 divided; row of thin spines on outer face alongside teeth. Mandible of paratype with 9 teeth, 7 of them simple. Maxillules of holotype (Fig.17H) bare along distal third of medial edge, then 2 rounded teeth separated by bifid tooth, former with 1 basal spine each, and 6 more proximal teeth, most of them terminally subdivided into 2-5 spinules. Maxillular teeth much weaker than those of mandible; row of tiny spines on outer face alongside teeth. Maxillules of paratype with 2 teeth between rounded ones, 5 proximal teeth with no more than 3 apical spinules, and 2 isolated basal spines; 2 submarginal comb rows of spinules. Maxillae fused into massive, triangular labium except for distal medial notch, tips not subdivided. Very large, unpaired lobe for maxillary glands between oral cone and thoracopods.

First thoracopods longest, setiform, others lobe-like, decreasing in length but not thickness posteriorly, sixth pair reduced to indistinct bumps, especially in paratype (Fig.17I,J). Seminal receptacles in thorax, 8 seen on left side of holotype, seemingly associated with bases of second and third thoracopods (Fig.17D).

Penis phallus-shaped, curving upwards distally, reaching to base of maxillae in holotype, but only as far as maxillary gland swelling in paratype (Fig.17D,K). Rami short, broad, and rounded, extended in holotype, partly bent down in paratype, each ramus with about 16 short setae in holotype, perhaps 12 in paratype (half that number seen on left ramus). Shaft with few ventral setae distributed along whole length in holotype, only on distal half in paratype.

**Remarks.** This interspecific comparison is based primarily on Grygier (1985b). The new species differs from *P. morula* Grygier in having a smooth rather than macroscopically bumpy carapace. It differs from *P. azorica* Grygier in having only one third as many teeth on the mandibles and maxillules, in lacking a diversity of spines and papillae on the carapace, and having round rather than square furcal rami. *Petrarca*

**Fig.17.** *Petrarca sensoria* n.sp., holotype (AM P37804) except for E, paratype (AM P37806). A–B, lateral and dorsal views of carapace. C, ventral half of left valve. D, main body, antennules omitted. E–F, left antennules in medial view. G–H, left mandible and maxillule, respectively, each with enlargement of medial armament (submarginal spinules in H actually on far side). I–J, left and right thoracopod clusters. K, abdomen and penis. Abbreviations as in Fig. 16, with ab, abdomen; oc, oral cone; ph, pharynx. Scale bars in mm.

*indica* Grygier has a long aesthetasc on the claw guard, but it has minutely denticulate medial edges on the paired mouthparts, a more slender penis, and much more massive ventrolateral carapace spines. Similarly, *P. bathyactidis* Fowler has massive ventrolateral carapace spines; it also has a short claw guard aesthetasc, a squared-off end of the penile shaft, and, at least in the holotype, apically bifid first thoracopods.

The differences between *P. sensoria* and *P. okadai* are rather subtle. Those that seem to be most trustworthy are large carapace papillae lying along the middle part of the ventral carapace margins instead of anteroventrally, taking the place of a nubbly ventral flange; hairs only in one row alongside of the mandibular teeth rather than on both sides and amongst them; much shorter spinules alongside the maxillular teeth; and much broader penile rami. The first thoracopods are usually shorter in *P. okadai*, and no spinule next to the claw guard's aesthetasc has been seen in that species.

Corals of the genus *Fungiacyathus* are well-known hosts of Petrarcidae worldwide (Zibrowius & Grygier, 1985), inhabiting internal galls that involve the columella, septa, and thecal wall, but the responsible crustaceans themselves have only rarely been found. Most records involve *F. marenzelleri* (Vaughan) from depths greater than 2000 m or not fully identified corals comparable to that species, such as the host of *P. bathyactidis* from off Japan. Previously recorded shallow *Fungiacyathus* with galls from which no parasites were recovered include *P. paliferus* (Alcock) in the Indian Ocean off Reunion at 280 to 375 m and an unidentified form off South Africa at 99 m (Zibrowius & Grygier, 1985; Cairns, 1989).

**Etymology.** From Latin *sensus* (sense), referring to the long sensory aesthetasc on the claw guard.

### *Petrarca goanna* n.sp.

Figs 18,19,21A,B

**Type material.** Fifteen specimens (6 pairs, 1 trio), HOLOTYPE the larger of pair 3 (AM P37810), other 14 specimens PARATYPES (AM P37811-P37818), occupying 7 external galls (*sensu* Zibrowius & Grygier, 1985) in *Turbinaria reniformis* Bernard (AM G15234, including gall of holotype), J.K. Lowry, R. Springthorpe & M.J. Grygier, 14 Feb. 1987, near entrance to Blue Lagoon, Lizard Island, Qld, 2 m.

**Other material.** Three galls from same collection remain unopened, and 2 additional pairs of parasites were given to Drs J.M. Healy and D.T. Anderson (University of Sydney) for eventually unsuccessful spermatological study.

**Diagnosis.** Carapace with series of radially directed, dorsal and posterior ridges formed from partly or fully coalesced, lumpy surface irregularities; margins crenulated due to protruding outer ends of ridges. Irregular anterolateral lumps on carapace with prickly surface texture but no ventral papillae or spines present. Maxillae mostly exposed due to very short lateral extensions of labrum. Mandibles and maxillules with about 20 teeth, those of mandibles longer and stronger, those near base of maxillules tending to form 2 rows. First thoracopods setiform or absent, remaining 4 or usually 5 pairs of thoracopods long, slender, unsegmented, naked, arising in tight cluster, sixth pair markedly shorter than others when present. Penis with small, squarish rami bearing many short setae. Posterior part of abdomen extremely small, at least 2-segmented with variable number of tiny spines.

**Host-parasite relations.** Live host material on hand included several broken pieces and one whole colony; the latter had six galls, including two empty ones on a dead, overgrown part. Galls were detected by a SCUBA diver running his hand over the smooth, acalicular side of a *Turbinaria* colony, while feeling for rounded lumps. While fresh and presumably still alive, these lumps were partly cut in half with a rock saw, then split with a sharp blow to expose the contents. Some proved to be overgrown coral barnacles, but others contained ascothoracidans, usually a pair. Ascothoracidan galls were up to about 4 cm across and were evident on the calicular or acalicular side of the coral, or both (Fig.21A,B). The texture of the coenenchyme of such a gall is coarser than its surroundings, and no calices open upon a gall. No galls contained brooded eggs or larvae. Shrinkage of the parasites and loss of their pink colour after preservation were evident.

**Description.** Holotype 5.87 mm long, 5.14 mm high in preserved state. Other specimens of pairs 1-6 3.73-6.93 mm long, 3.75-6.35 mm high, measurements of width not comparable due to different degrees of valve splaying. Among all specimens, height 85-110% of length (mean percentage 94). In pairs 1-6, respectively, smaller specimen 90, 76, 75, 84, 83, and 88% as long as larger one. Carapace roughly spherical when valves not splayed, with lumpy external appearance and no distinct hinge (Fig.18A,B). Five to 8 radial ridges formed of partially to fully coalesced lumps in fan-like array encompassing anterodorsal to posteroventral regions, coalescence less pronounced anteroventrally along each ridge. In medial view (Fig.18C), valve margins appearing crenulated due to same ridges, latter barely protruding medially, and distinct only outside arc of dorsum of main body. Additional lateral swellings with prickly surface in anteroventral quadrant of valves. Ventral margin smooth, without papillae or spines.

Body enclosed between carapace valves except for tip of penis (Fig.18C,D). Body grub-like, consisting of anterodorsally attached head with antennules and oral cone, ovoid, apparently 2-segmented thorax with tight ventral cluster of slender thoracopods, and abdomen with massive, penis-bearing first segment and vestigial rear

**Fig.18.** *Petrarca goanna* n.sp. A, holotype (AM P38810), left lateral view; B–C, paratype (AM P37811 or P37812), dorsal view and with left valve removed to expose body, respectively. D, body of holotype with details of antennular seta and E, of distal part of right antennule. F, labrum and G, tip of penis of two paratypes (AM P37811 and P37812). Abbreviations as in Fig. 16, with an, antennule. Scale bars in mm.

**Fig.19.** *Petrarca goanna* n.sp., paratype pair (AM P37811, AM P37812) except I, different paratype (AM P37812). A–B and C–D, two sets of medial edges of mandibles (A, C) and maxillules (B, D). E, maxillae. F–G, right and left thoracopods, respectively, from one specimen, and H, right thoracopods from other, all showing seminal receptacles. I–J, vestigial posterior abdomens. Scale bars in mm.

portion. In holotype, body length about 2.85 mm from front of oral cone to rear of first abdominal segment, this distance in 4 different specimens equal to 49-61% of carapace length.

Antennules 5-segmented with little armament, somewhat prehensile, segments becoming narrower distally (Fig.18D). First segment with lateral condyle and second with narrow, sclerotised medial strip; third segment triangular; fourth with curved posterior margin and short, straight, anterior margin, short seta at corner between anterior margin and oblique distal margin (seen in only 2 of 3 examined antennules). Fifth segment rectangular, with heavy, curved claw on anterodistal corner and longer, laterally flanged claw guard on posterodistal corner (Fig.18E). Probably 3 vestigial setae at base of claw and to each side. Claw guard with up to 4 vestigial, distal setae, subapical aesthetasc not over half as long as claw guard proper.

No eyes or frontal filaments present.

Oral cone short but very deep, consisting of massive labrum, massive labium formed from fused maxillae, and 2 sets of paired mouthparts. Labrum prow-shaped with thickened anterior surface and short posterolateral extensions leaving maxillae and bases of paired mouthparts largely uncovered (Fig.18D,F). Mandibles and maxillules based on pair 1 (Fig.19A-D). Both with rounded posterolateral margin and straight, toothed medial edge, maxillule more pointed distally. Mandibles with 20-25 straight, narrow teeth, some proximal ones bifid; a few additional, small spinules also present. Maxillules with about same number of teeth, but only about half as long; distal ones often rounded with terminal point, proximal ones tending to overlap as though formed into 2 irregular rows. Maxillae forming trapezoidal floor of oral cone, ending in 2 pairs of very short, rounded lobes perhaps representing bifid tips of generalised maxillae (Fig.19E).

Thorax unsegmented, but triangular region of thinner cuticle found at rear. Remainder of thorax somewhat bulbous, thoracopods in tight cluster below its rear half, female gonopore located in front of them (Fig.18D). Thoracopods not appearing to arise in orderly sequence in lateral view, but in ventral view seen to be paired but staggered; possibly thoracopods 3 and 4 usually positioned more medially than other pairs. Four to 6 thoracopods present on each side of body, varying among specimens (Fig.19F-H). Setiform thoracopod I rarely present, only on left side of 2 of 6 closely examined specimens, absent on both sides of holotype. Thoracopods II-V always present, as long, narrow, unsegmented, unarmed, distally blunt lobes. Thoracopod VI absent on both sides of smaller specimen of pair 1, but otherwise present at least as nub, generally similar in shape but shorter than other thoracopods. Numerous cylindrical seminal receptacles arranged in batteries in thorax above thoracopods, possibly some associated with each of thoracopods II-V.

First abdominal segment large, supporting long, thick, terminally bifid penis (Fig.18D). Shaft of penis slightly arcuate, narrowed at midlength, thickened anteriorly; cluster of short setae on squared-off tip, additional setae on distal half of ventral side; one penis seen with considerably larger seta below terminal cluster, between bases of rami (Fig.18G). Small, squarish rami arising posteroventrally from end of shaft, bearing numerous short setae (13-20) similar to or little shorter than those on shaft.

Rest of abdomen vestigial, apparently 2- or 3-segmented (only 2 segments clearly seen) generally sunken into posteroventral part of first segment, but occasionally protruding (Fig.19I,J). Second (or third?) segment possibly actually short, rounded, furcal rami. From 1-4 tiny terminal spines counted in different individuals, perhaps not all arising from same sites.

**Remarks.** The only described species of *Petrarca* comparable to *P. goanna* n.sp. is *P. morula*, which was discovered in external galls of *Turbinaria* sp. from the Banda Islands, Indonesia (cf. Grygier, 1985b). *Petrarca goanna* is larger, the largest type specimen of *P. morula* being 3.8 mm long. The carapace of the new species differs in having a much more regular pattern of external lumps, a crenulated valve margin, and no ventral papillae. It also has about twice as many teeth on the mandible and a clearer maxillular dentition. No first thoracopod was seen in *P. morula*.

The intermittent appearance of the first and sixth thoracopods in *P. goanna* confirms doubts raised above about the utility of the number of thoracopods in diagnosing species of Petrarcidae, as Grygier (1985b) did, for example. It also casts doubt on whether Grygier (1985b) correctly identified the thoracopods in different specimens of *P. azorica*. Supposedly that species has thoracopods II-VI only. A setiform first leg on one side of the holotype was identified as a shrivelled second thoracopod, but it is possible that that was actually thoracopod I, and that thoracopod VI was absent on that side.

*Turbinaria* spp. often serve as hosts of Petrarcidae. Numerous examples of petrarcid galls on dried specimens of this coral genus have been found in various museums (herein, below). They can be distinguished from galls formed by cryptochirid crabs since they have no external opening. Sometimes they resemble overgrown coral barnacles, but the latter are usually more conical, and plates of the barnacle wall are found inside when the "gall" is split. In contrast, petrarcid galls are normally rounded or oval, may penetrate all the way through the coral, and within them there are usually two linked cavities whose contours follow the parasites' carapaces.

### *Petrarca* sp.

Figs20,21C

**Material examined.** 2 specimens (AM P39495-6) from dried *Anthemiphyllia dentata* Alcock (AM G15235), F. Rowe & P. Colman, *Kimbla* Stn 3, 17 Nov. 1977 (#2639), 33.8 km east of Lady Musgrave Island, Qld,

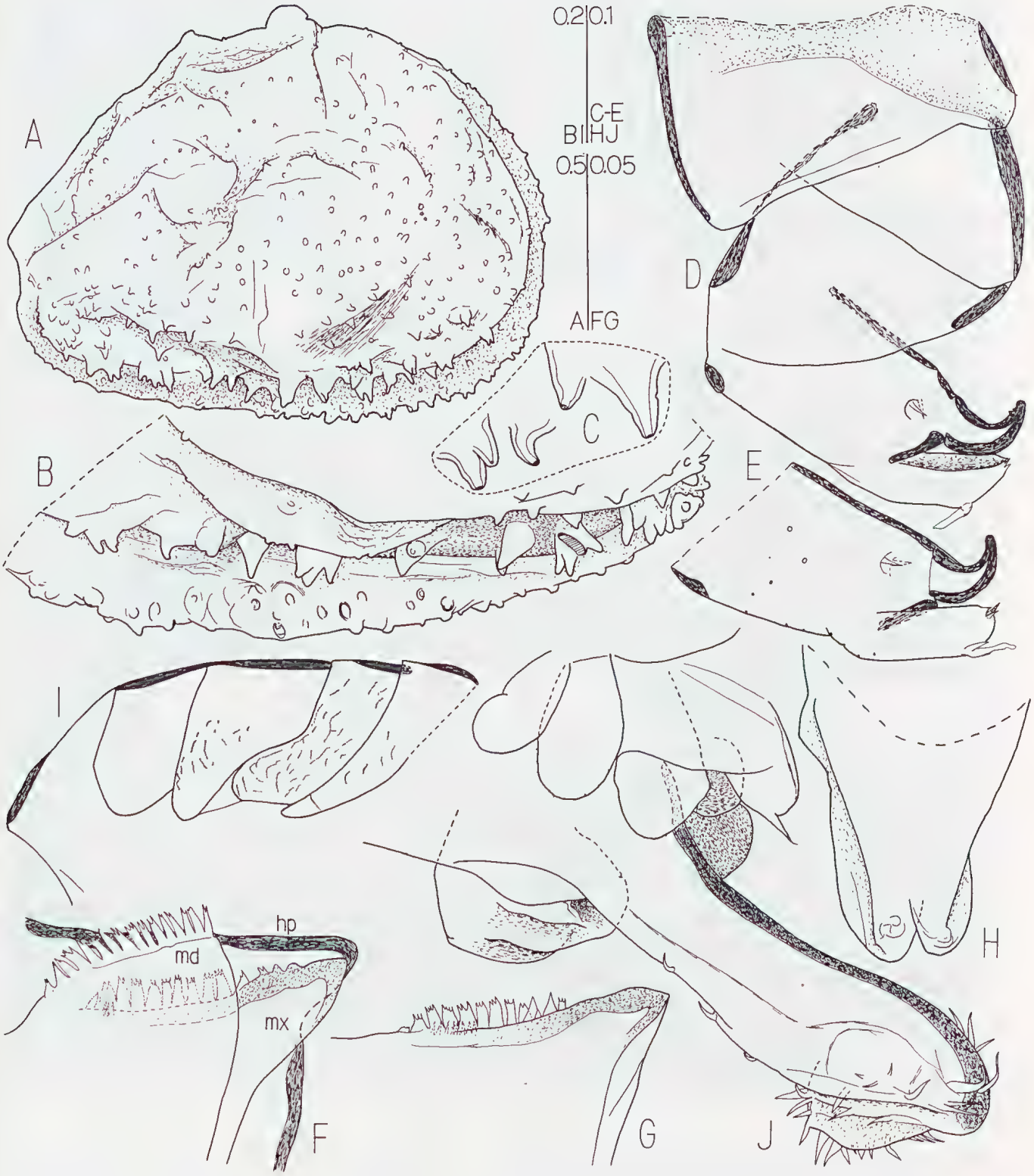


**Fig.20.** *Petrarca* sp. (mostly AM P39496, but B–C based on AM P39495) A–C, carapace: A, lateral view, front end left; B, armament of ventral valve margin; C, spines apparently with apical pores. D–E, antennules: D, left one, medial view; E, distal segment of right one, lateral view. F–H, mouthparts: F, hypopharynx (hp), mandible (md), and maxillule (mx); G, other maxillule; H, maxillae, frontal view. I, four thoracic tergites and first abdominal segment. J, thoracopods, abdomen, and penis. Scale bars in mm.

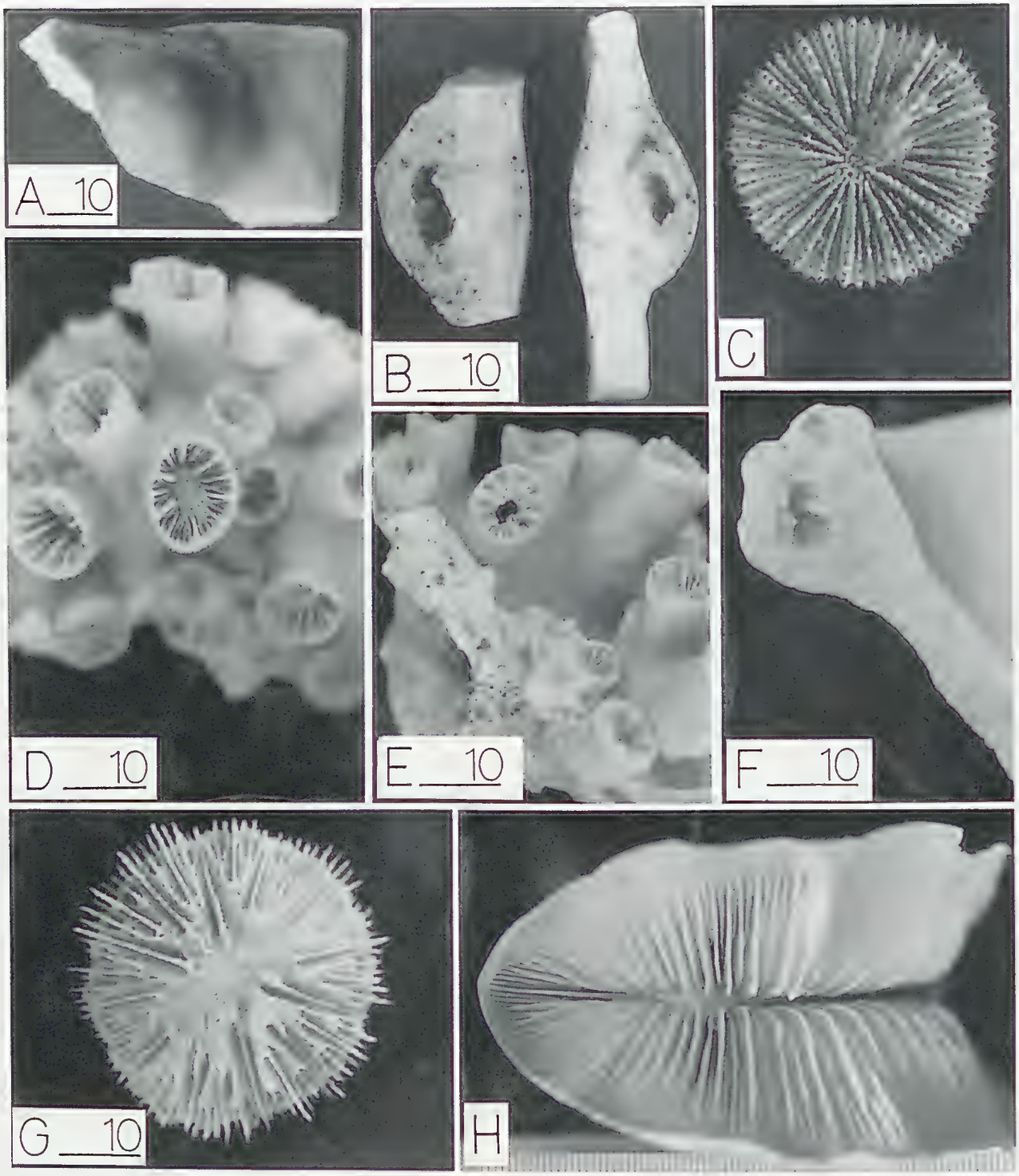


**Fig.21.** Australian Scleractinia with petrarcid galls. A–B, *Turbinaria reniformis* Bernard from Lizard Island, Qld (Australian Museum) with galls caused by *Petrarca goanna* n.sp. (AM P37810-18), those in B opened to show internal cavity. C, *Anthemiphyllia dentata* Alcock from off Qld (USNM 78611), unopened gall, photograph supplied by S.D. Cairns without scale. D–E, *Dendrophyllia* sp. from Dampier Arch., WA (National Museum of Victoria, uncatalogued): D, showing calice with enlarged columella; E, showing opened, infected calice. F, *Turbinaria conspicua* Bernard from Dampier Arch., WA (WAM 531-78) with open petrarcid gall combined with coral barnacle. G, *Deltocyathus magnificus* Moseley from north-west of Augustus Island, WA (WAM 524-81(1)) with greatly enlarged, irregular columella. H, *Flabellum magnificum* Marenzeller from off Cape Leveque, WA (WAM 580-84)) with gall in columella. Scale bars in mm.

23°33.7'S 152°37'E, 348-339 m; 3 specimens (AM P39497) from dried *A. dentata* (AM G15264), A.A. Racek, Night Challenge Trawl 318, 2 July 1959, east of Newcastle, NSW, 156-60 fms (285-110 m). Despite efforts to rehydrate the 5 dried ascothoracidan specimens in detergent, none found suitable for naming as holotype or as syntypes. This coral species ordinarily without columella and with dentate septa meeting in center, but infested ones with spongy internal gall (*sensu* Zibrowius & Grygier, 1985) close to center of calice (Zibrowius, personal communication).

Two dry specimens of *A. dentata* in National Museum of Natural History, Smithsonian Institution, with unopened, excentrically placed galls tentatively attributed to same parasite as above, gall on one specimen occupying about one third of radius (Fig.21C): USNM 78611, A.J. Bruce, Nimbus-12, off Qld, 27 July 1968, 26°32'S 153°50'E, 275 m; USNM 78609, A.J. Bruce, Nimbus-55, 5 Aug. 1968, off Qld, 26°27'S 153°50'E, 270-272 m.

**Description.** All 5 specimens shrivelled due to drying, with little improvement after soaking in detergent; P39495-6 in somewhat better condition, but no specimens with thoracopods, posterior part of abdomen, and distal end of penis well displayed.

Carapace probably subglobular in life, greatest girth at about 30% of height (Fig.20A). Length and height of P39495-6 1.28 *x* 0.87 mm and 1.54 *x* 1.11 mm, respectively; one specimen from P39497 2.27 *x* 1.91 mm, others similar; all specimens undoubtedly larger in fresh condition. Carapace bivalved but lacking distinct dorsal hinge. Free margins with distinct papillose flange most of way around, similar papillae scattered over dorsal two thirds of valve surfaces, giving way ventrolaterally to much larger, blunt, broad-based and often irregularly compound spines, at least some larger spines apparently with pore at tip (Fig.20B,C). Longest spines about 90 µm. Upper two thirds of carapaces of some specimens (P39497) filled with developing oocytes, but precise arrangement of internal organs not studied.

Main body semicircular with anterodorsal cephalic attachment zone. Head making up half of body of measured specimen from P39497, body measuring 1.45 mm long from front of oral cone, 1.38 mm high including penis. Head with massive, folding antennules and short, blunt oral cone. Thorax with at least 4, maybe 5, distinct tergites (Fig.20I), anterior ones narrower and with their ventral parts curving posteriorly, curved rows of minute cuticular ctenae laterally on tergites. Number of lobe-like thoracopods unclear (details below). Very large first abdominal segment bearing massive, distally swollen, more or less straight penis (Fig.20J). Rest of abdomen vestigial, sunken into rear of first segment, number of segments unknown.

Antennules of P39495-6 examined (Fig.20D,E), 5-segmented, with L-shaped, sclerotised part of first segment wider than long. Second segment quadrilateral with anterior margin about half as long as posterior; third segment more or less triangular. Fourth segment with extremely short anterior margin, oblique distal edge set at 45° angle to anterior side, and posterior edge about as long as other 2 margins combined; this segment apparently unarmed in one specimen, but with short seta proximally on lateral ridge of oblique distal side in other. Last segment parallelogram-shaped and slightly tapered, with several pores on lateral face; bearing heavy claw with or without 2 blunt denticles; 2 short setae lateral and medial to base of claw, no marginal one seen; claw guard about twice as long as claw, with lateral flange, 2-4 tiny apical setae, and short, subapical aesthetasc accompanied or not by short seta.

Labrum of P39496 about 0.30 mm long and deep, lateral edges flanking sides of maxillae, anterior face bent at obtuse angle about one third of distance from base. Mouthparts of same specimen dissected free (Fig.20F-H). Mandibles and maxillules both with short, broad, muscular base and short, dentate medial edge not extending beyond end of hypopharynx, medial edge of mandible half as long as that of maxillule. Mandible with 16 teeth, mostly bifid or trifid apically; maxillule with 12-14 teeth along middle half of medial edge, tips mostly truncate with 2-4 apical denticles. Maxillae forming massive, trapezoidal labium, rounded tips with anterodistal bump on each side.

Number of thoracopods unclear, 4 or 5 lobe-like ones per side, decreasing in size posteriorly (Fig.20J). Tip of apparent first right thoracopod of P39496 produced into short setiform process on lobelike base, but no setiform first thoracopods as known in other petrarcids observed.

Penis (Fig.20J) with short, ventral setae along shaft, only 1 distal ramus clearly seen in each of 2 specimens, ramus and rounded tip of shaft with numerous short setae, ramus capable of swinging nearly 180°, judging from different positions in various specimens. Posterior part of abdomen of P39495-6 examined closely, former with 4 short setae or spines, their precise positioning unclear, latter with no apparent armament (Fig.20J).

**Remarks.** The clearly segmented thorax distinguishes these specimens from all other species of *Petrarca*, in which the only evidence of thoracic segmentation is limited to dorsal cuticular thickenings, occasional dorsal wrinkles, and musculature (Okada, 1938; Grygier, 1985b, herein above). Clear segmentation has been considered a diagnostic feature of the other petrarcine genus, *Zibrowia* Grygier, but at least two of the other major distinctions between the two genera are still valid: the present specimens have no posterior lobes on the carapace and their abdomen does not end in a prominent single spine; the tip of the penis is not displayed well enough to be sure whether it is biramous or not.

*Petrarca okadai* is the only other species with papillae all over the carapace in some cases, but the papillae are not replaced by such large spines ventrolaterally. The outline of the fourth antennular segment, especially the short anterior margin, is most similar to that of *P. bathyactidis*, the type species of the genus, whose carapace has large, ventrolateral spines like the present ones, but the dorsal half of its carapace is bare of papillae, and the tip of its penis is squared off (Grygier, 1985b). The present mandibular dentition is so

far unique in the genus (mouthparts of *P. bathyactidis* unknown), but the maxillular dentition is similar to that of *P. okadai* and *P. sensoria* n.sp.

This is the second record of *Anthemiphyllia dentata* as a host of Petrarcidae. Zibrowius & Grygier (1985) reported empty internal galls in that species from 290 to 350 m off New Caledonia.

## Other New Indo-Pacific Records of Petrarcid Galls in Scleractinian Corals

The following listing supplements the catalogue of petrarcid galls in scleractinians published by Zibrowius & Grygier (1985). Some of the entries were kindly provided by Dr H. Zibrowius, who has sent me the contents of galls discovered in the course of his recent studies of Indo-Pacific ahermatypic corals. The other entries are based on my own observations in various museums, mostly in Australia. In two cases (1 and 5), well preserved parasites were recovered from the galls but have not yet been studied in detail. *Turbinaria* always has external galls (*sensu* Zibrowius & Grygier, 1985), and the other corals have internal galls. To avoid damage to the hosts, most of the intact galls in dried museum specimens were not opened, and only the largest galls observed in *Turbinaria*, about whose etiology I have little doubt, are listed here.

1. (Zibrowius, personal communication) *Balanophyllia* sp. (i.e., solitary dendrophylliid), J. Vacelet, Gulf of Tadjoura, Obok, Djibouti, under small overhang, 15 m. Very distinct internal gall inside calice and independent of columella. Spongy proliferation extending up side from above columella to calicular edge, cavity involving septa only. After NaOCl treatment proliferation detached, leaving nearly normal columella. Gall very peripheral and visible from outside as modification of wall surface. Contained 2 unidentified specimens of *Petrarca*.

2. Dried colony labelled "*Dendrophyllia* sp.," National Museum of Victoria Acc. no. 78/9, uncatalogued (Australasian Marine Photographic Index Madro. 201)), N. Coleman, 1 Nov. 1971, Kendrew Island, Dampier Archipelago, Dampier, WA, reef, in cave, 8 m. At least 3 of about 50 calices with internal galls, visible externally as proliferation of columella upwards into septa, higher on one side of calice (Fig.21D). One opened gall (Fig.21E) with bilocular cavity and 2 dried specimens of *Zibrowia* sp. with eggs.

3. (Zibrowius, personal communication). Orange-pink *Dendrophyllia* sp., colonial but with spreading stolons as well as buds, H. Zibrowius, May 1985, small island (Manu-Manou) south of Capsalon Island, off Danlig village, in Dumaran Passage, north-east Palawan, Philippines, about 10°33'N 119°42.5'E, small overhangs at 3-5 m. Empty gall cavity deep down within or below columella, latter not markedly modified from above.

4. (Zibrowius, personal communication) *Tubastraea* sp. (perhaps young colony of *T. micranthus* (Ehrenberg) [= *T. nigrescens* (Dana)]), same locality as 3. Only parasite eggs recovered from within internal gall below one calice.

5. (Zibrowius, personal communication). Orange, plocoid to phaceloid *Tubastraea* sp., same locality as 3. Calices normally with reduced, deeply sunken columella, but 2 infested calices in one colony with large, spongy columella visible despite coral tissue, containing respectively 2 and 3 individuals of *Zibrowia* sp.

6. Dried *Enallopsammia rostrata* (Pourtalès) (i.e., *E. amphelioides* (Alcock)), Bernice P. Bishop Museum, uncatalogued, S. Ralston, HURL Dive 83-191, 30 Sept. 1983, Johnston Atoll, 16°41.4'N 169°24.9'W, 354 m on 30-45° slope. Four of 6 pieces in lot bearing numerous spongy and sealed external galls like those previously seen on this host genus in the Atlantic and Pacific (see Zibrowius & Grygier (1985) and references therein). Largest spongy gall 22.5 mm, largest sealed one 27 mm.

7. Dried *Turbinaria conspicua* Bernard (WAM 531-78), L.M. Marsh, 9 Aug. 1978, south-west corner of Dolphin Island, Dampier Archipelago, 4.5 m. Specimen bearing half of a split, bilocular gall combined with a coral barnacle (Fig.21F).

8. Dried *Turbinaria frondens* (Dana), WAM 12-83(1), J. Fromont, *Soela*, 30 July 1982, 15.7 km north-west of Port Hedland, WA, 20°12'S 118°29'E. One very large gall and maybe 2 small ones.

9. Dried *Turbinaria frondens*, Queensland Museum uncatalogued, I. Neuss, 18 Dec. 1971, Tryon Reef, MEQ, north-west side, outer slope, high tide, 3-9 m. Oval spongy region 21 *x* 10.5 mm, with about 6 mm wide raised knob in center.

10. Dried *Turbinaria danae* Bernard, Queensland Museum G7095, J. Veron *et al.*, 1972, Solitary Islands, 30°01-14'S. Three spongy petrarcid galls: one measuring 31 *x* 17.5 mm, low and involving both surfaces; another within a fold; third one irregular and near bottom of cup-shaped colony on calicular side.

11. Dried *Turbinaria peltata* (Esper), probably misidentified, Zoological Museum, Leningrad, no. 45 in public display case, no data. Opened bilocular gall on outer, acalicular side of conical colony.

12. Dried *Turbinaria* sp. (AM 13860), F.H. Talbot & M. Cameron, 4 Oct. 1967, outer north-west face of reef, One Tree Island, Capricorn Group, Qld, 3-12 m. Big gall principally in calicular side of broken slab, 2 linked cavities with bumpy walls and orange discolouration containing unidentifiable fragments of parasite (not *Zibrowia*).

13. Dried *Turbinaria* sp., South Australian Museum uncatalogued, no data. Stalked disc with 4 major and several minor vanes, one gall on rear near stalk, other on medial edge of vane.

14. Dried, chalice-shaped *Turbinaria* sp., South Australian Museum uncatalogued, Broome, WA, presented by J.C. Capper. Low and wide, spongy, large gall on upper side.

15. Large, dried, cup-shaped *Turbinaria* sp. (USNM uncatalogued), J.B. Steere, about 1900, Philippines. Large gall.

16. Dried *Turbinaria* sp., uncommon species different from 17 and 18 below, University of Guam Marine

Laboratory (UOG) 5193 (old number UOG 74B & C), R.H. Randall & Y.M. Cheg, 23 Jan. 1975, Stn 27, Nan Wan Bay at Ch'uan Fan-Shir, south coast of Taiwan, seaward side of offshore islet, 4 m. Single oval, external gall affecting both sides of coral, calicular side 14 *x* 12 mm with calices around edges, acalicular side 15 *x* 9 mm.

17. Dried *Turbinaria* sp., common species, UOG 13848, R.H. Randall, 30 July 1979, Lanyu Island (ie., Orchid Island), Taiwan, reef front slope on wall of large hole, unshaded, 4 m. Two spongy-textured, oval, external galls close together and affecting both sides of thin coral, calicular sides 12 *x* 9 mm and 13.5 *x* 10 mm, 3.5-4 mm high, acalicular sides respectively 16 *x* 11 mm and 16 *x* 8 mm.

18. Dried *Turbinaria* sp., same common species as 17, UOG 5422 (old number UOG 304), R.H. Randall & Y.M. Cheng, 26 Jan. 1975, Stn 30, Tan'tzu, south coast of Taiwan, edge of channel on reef front, unshaded, 3.5 m. Spherical gall 12.5 mm in diameter, affecting both sides of coral, with bilocular cavity containing shrivelled remains of two individuals of ?*Petrarca* sp.

19. Dried *Deltocyathus magnificus* Moseley (WAM 524-84(1)) (determined by S.D. Cairns from photo; Fig.21G)), S. Slack-Smith, *Soela*, 14 Feb. 1984, Stn SO 01/84/077, north-west of Augustus Island, WA, 13°33.3-34.3'S 122°54.5-52.3'E, 394-390 m. Enlarged, irregular and spongy, excentric columella.

20. Dried *Flabellum magnificum* Marenzeller (WAM 580-84) (determined by S.D. Cairns from photos; Fig.21H), S. Slack-Smith, *Soela*, 12 Feb. 1984, Stn SO 01/84/064, north-west of Cape Leveque, WA, 14°50.2-48.6'S 121°31.4-33.2'E, 356 m. Enlarged columella growing up into septa as lump on one side.

21. (Zibrowius, personal communication) *Flabellum* sp., MUSORSTOM 2, Stn 83, 2 Dec. 1980, Philippines, 13°55.2-55.6'N 12°30.5'E, 318-320 m. Empty internal gall, expressed externally as spongy proliferation of normally deep-seated columella, extending higher up in infested part.

These findings confirm that petrarcid ascothoracidans are widespread and reasonably abundant in the tropical Indo-Pacific, particularly in representatives of the Dendrophylliidae (Numbers 1–18), and are especially common and obvious on many species of the important hermatypic reef coral genus *Turbinaria*. In addition to those listed, several other specimens of *Turbinaria* in the Western Australian Museum have small lumps which may, at least in part, be due to petrarcid infestation, and underwater photographs of Australian *T. mesenterina* (Lamarck) (Veron, 1986: 567, fig.1) and *Turbinaria* sp. from Taiwan (Fang & Hwang, 1987: 30, fig.1) also seem to show petrarcid galls. All the other genera in the list have been recorded as petrarcid hosts before (Zibrowius & Grygier, 1985), but *Deltocyathus magnificus* and *Flabellum magnificum* are new host species records.

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## APPENDIX 1

Table 1. *Gorgonolaureus decurvatus* n.sp., carapace size and brood of several type specimens (WAM 93-87), #1 and #2 dissected paratypes, #4 holotype.

| Specimen | Height | Length | Width(top) | Width(bottom) | Brood |
|---|---|---|---|---|---|
| #1 | 2.30 | 1.68 | 1.64 | 1.17 | 23 nauplii |
| #2 | 2.07 | 1.52 | ? | ? | >19 eggs |
| #3 | 2.11 | 1.57 | 1.43 | 1.15 | – |
| #4 | 2.40 | 1.70 | 1.61 | 1.21 | 12 nauplii |
| #5 | 2.33 | 1.74 | 1.62 | 1.22 | 48 nauplii |

Table 2. *Gorgonolaureus decurvatus* n.sp., thoracopodal setation of paratype #1 (WAM 93-87), ranges reflecting differences between left and right sides (only one each of pairs III and IV included), positions as marked in Fig.2C,D, parentheses used in case of 2-segmented endopods.

| Leg/ Position | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| I | 1 | – | – | 7 | 3 | (1) | | – | – |
| II | 1 | – | 1 | 8-9 | 3 | 1 | 1 | 4 | 2 |
| III | 1 | – | 1 | 9 | 3 | 1 | 1 | 3? | 2 |
| IV | 1 | – | 1 | 9 | 4 | 1 | 1 | 3 | 2 |
| V | – | – | 1 | 7-8 | 4 | 1 | 1 | 1 | 2 |
| VI | – | – | – | 7-8 | 4 | (1) | | 1 | – |

Table 3. *Gorgonolaureus vietnamianus* n.sp., left thoracopodal setation, conventions as in Table 2, with parentheses used for 1- and 2-segmented endopods.

| Leg/ Position | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Holotype (ZIN 1/66583) | | | | | | | | | |
| I | 1 | – | – | 7 | 2 | (1) | | – | – |
| II | 1 | – | 1 | 13? | 4? | 1 | 1 | 2? | 1 |
| III | 1 | – | 1 | 15 | 5 | 1 | 1 | 2? | 1 |
| IV | 1 | – | – | 13 | 5 | 1 | 1 | 2 | 1 |
| V | – | – | – | 14 | 5 | 1 | 1 | 2 | – |
| VI | – | – | – | 11 | 4 | (2) | | 2 | – |
| Paratype (ZIN 2/66584) | | | | | | | | | |
| I | 1 | – | – | 10 | | (2) | | – | – |
| II | 1 | – | 1 | 16 | 5 | 1 | 1 | 3 | 1 |
| III | 1 | – | 1 | 18 | 6 | 1 | 1 | 4 | 1 |
| IV | 1 | – | 1 | 16 | 6 | 1 | 1 | 3 | 1 |
| V | – | – | – | 15 | 6 | 1 | 1 | 2 | – |
| VI | – | – | – | 13 | 4 | (2) | | 2 | 1 |

Table 4. *Gorgonolaureus tricornutus* n.sp., unilateral thoracopodal setation of two paratypes (MNHNP Ci2048), conventions as in Table 2, but ranges indicating uncertainty and, at position 4, a+b+c referring to numbers of medial, apical, and lateral setae, respectively.

| Leg/ Position | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| Female | | | | | | | | | |
| I | – | 1 | – | 8 | 3 | (3) | | – | – |
| II | 1 | – | 1 | ? | 6 | 1 | 3 | 5 | 5 |
| III | 1 | – | 1 | 6+3+2 | 7 | 1 | 2 | 6 | 5 |
| IV | 1 | – | 1 | 7+3+2 | 8 | 1 | 2 | 6 | 4-5 |
| V | – | – | 1 | 7+3+2 | 8 | 1 | 0? | 3 | 2 |
| VI | – | – | – | 5+4+1 | 7 | (2) | | 4 | – |
| Male | | | | | | | | | |
| I | 1 | – | – | 3+3+2 | 2 | (5) | | – | – |
| II | 1 | – | 0-1? | 7+3+2 | 6-7? | 1 | 2 | 6 | 5 |
| III | 1 | – | 1 | 9+3+2 | 7 | 1 | 2? | 6 | 4 |
| IV | 1 | – | 1 | 7+3+2 | 8? | 1 | 2 | 4? | 5 |
| V | – | – | 1 | 8+3+2 | 8 | 1 | 1 | 4 | 1 |
| VI | – | – | ? | 6+4+2 | 8 | (3) | | 6 | – |

Table 5. *Flatsia walcoochorum* n.g. n.sp., left thoracopodal setation of holotype female (AM P37803), conventions as in Table 2, but ranges indicating uncertainty and parentheses used in cases of reduced segmentation.

| Leg/ Position | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 |
|---|---|---|---|---|---|---|---|---|---|
| I | 15 | – | – | >23 | >13 | (–) | | – | – |
| II | – | – | – | 17 | 14 | 3 | 7 | 15? | >3 |
| III | – | – | 1* | 19 | 16-17 | 3 | 5 | 15 | 3 |
| IV | – | – | 2* | 18 | 19 | 4 | 7 | 18 | 8 |
| V | 1 | – | – | 11 | >13 | (4) | | 10 | 7 |
| VI | (2) | | (21) | | (6) | | – | (1) | |

*including 1 medial seta.

# The Nereididae (Polychaeta) from Australia – *Leonnates*, *Platynereis* and *Solomononereis*

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ABSTRACT. *Leonnates crinitus* n.sp., *L. bolus* n.sp. and *Platynereis uniseris* n.sp. are described from Northern Australia. A systematic account of *Leonnates*, *Platynereis* and *Solomononereis* known from Australia and a key to species recorded from Australia is provided.

HUTCHINGS, P.A. & A. REID, 1991. The Nereididae (Polychaeta) from Australia – *Leonnates*, *Platynereis* and *Solomononereis*. Records of the Australian Museum 43(1): 47–62.

In this paper, the second in a series to describe the nereidid fauna of Australia, *Leonnates*, *Platynereis* and *Solomononereis* are discussed. We describe 11 species, three of which are new: *Leonnates crinitus* n.sp., *L. bolus* n.sp. and *Platynereis uniseris* n.sp. *Leonnates jousseaumei* Gravier and *Solomononereis marauensis* Gibbs are new records for Australian waters.

A key to the genera of nereidids occurring worldwide is given by Fauchald (1977). In the final paper of this series on Australian nereidids, a key to the genera and species occurring in Australia will be given.

The three genera discussed in this paper, belong to two groups identified by Fitzhugh (1987) as being closely related to one another. The two other genera in these groups *Perinereis* and *Ceratonereis* which are both extremely well represented in Australian waters, form the basis of other papers (Hutchings *et al.*, in press; Hutchings & Reid, in preparation).

We have used the terminology described in the first paper on the Gymnonereidinae (Hutchings & Reid, 1990). The following abbreviations have been used in the text: AHF - Allan Hancock Foundation, Los Angeles, California (Polychaete collections now located at the Los Angeles County Museum); AM - Australian Museum, Sydney; BMNH - British Museum (Natural History), London; NMV - National Museum of Victoria, now Museum of Victoria, Melbourne; NTM - Northern Territory Museum, Darwin; QM - Queensland Museum, Brisbane; SAM - South Australian Museum, Adelaide; SSM - Naturhistoriska Riksmuseet, Stockholm; TASM - Tasmanian Museum, Hobart; USNM - National Museum of Natural History, Smithsonian Institution, Washington D.C.; WAM - Western Australian Museum, Perth. Non-Australian distributions are in most cases based on the literature, whereas Australian distributions are based upon material examined. Where information was available, depths and dates of collection are given with each specimen examined.

### *Leonnates* Kinberg

*Leonnates* Kinberg, 1866: 168.–Fauchald, 1977: 89.

**Type species.** *Leonnates indicus* Kinberg, 1866, by original designation.

**Diagnosis.** Prostomium with 2 antennae, bi-articulate palps, 2 pairs of eyes. Oral ring of pharynx either smooth, or with soft papillae. Maxillary ring with paragnaths or papillae. Four pairs of tentacular cirri, parapodia biramous. Notosetae homogomph spinigers, neurosetae heterogomph falcigers with coarsely serrated blades.

**Remarks.** Fauchald (1977) records that ten species of this genus have been described. No comprehensive revision of the genus has been undertaken. The majority of species have been described from the tropics.

### Key to Australian Species of *Leonnates*

1. Area V of pharynx with papillae ..... *Leonnates stephensoni*

—— Area V of pharynx without papillae ..... 2

2. Maxillary ring paragnaths of Areas I-II and III-IV in continuous bands ..... *L. bolus* n.sp

—— Maxillary ring paragnaths of each Area in discrete clusters ..... 3

3. Neuropodial falciger blades boldly serrated with pointed terminal tooth. Notopodial falcigers present posteriorly ..... *L. jousseaumei*

—— Neuropodial falciger blades finely serrated with blunt terminal tooth. Notopodial falcigers absent ..... 4

4. Area I of pharynx without paragnaths, Area III with 6-16 paragnaths ..... *L. decipiens*

—— Area I of pharynx with paragnaths, Area III with 25-40 paragnaths ..... *L. crinitus* n.sp.

### *Leonnates bolus* n.sp.

Fig.1a–h

**Material examined.** HOLOTYPE: Northern Territory, Darwin Harbour, East Arm, 12°30'S 130°55'E, mangroves, 14 Dec. 1984, 1(NTM W2518) 50 mm long, 2 mm wide, 1.3 mm jaw length, 120 setigers, complete. PARATYPES: Western Australia, Admiralty Gulf, Port Warrender, 14°35'S 125°53'E, Oct. 1976, 1(WAM 422-86) 42 mm long, 3 mm wide, 1.6 mm jaw length, 68 setigers, incomplete; 1(USNM 127644) 52 mm long, 2.4 mm wide, 1.5 mm jaw length, 88 setigers, incomplete.

**Description.** Colour in alcohol cream. Prostomium rectangular with deep median furrow, eyes black with distinct lenses, anterior pair largest. Palps cylindrical with globular palpostyles; antennae conical, extending to tip of palps (Fig.1a). Dorsalmost pair of tentacular cirri longest, broken in the holotype, extending approximately to setiger 19 on paratype material. Jaws robust, heavily sclerotised, with 10 fine teeth. Pharynx with paragnaths on maxillary ring arranged as follows: Area I = 18, II = 9, III = 35, IV = 9; paragnaths in Areas I-II in continuous band 2-3 deep, with paragnaths in Area II larger than those in Area I. Similar arrangement ventrally. Areas I-II and III-IV separated by gap laterally (Fig.1a-b). Oral ring with papillae arranged as follows: Area V = 0, VI = 2, VII-VIII = 8. Oral ring with papillae arranged in 2 rows, row of large blunt papillae in an evenly spaced band in centre of ring and row of small, conical, sharply pointed papillae close to intersection of oral and maxillary rings (Fig.1a-b).

Anterior notopodia with broad based, conical dorsal ligule, narrow, shorter conical median ligule and long

tapering dorsal cirrus that greatly exceeds length of dorsal ligule (Fig.1c-d). Low, rounded superior lobe present. Neuropodia with narrow, conical superior and inferior lobes; superior lobe slightly shorter than inferior lobe. Postsetal lobe conical, shorter than acicular lobes. Ventral ligule short, conical. Narrow tapering ventral cirrus. Median and posterior parapodia with lobe proportions as for anterior parapodia but with all lobes decreased in size. Anal cirri long, fine, as long as last 12 setigers. Notosetae homogomph and heterogomph spinigers; neurosetae homogomph and heterogomph spinigers in supra-acicular fascicle, heterogomph

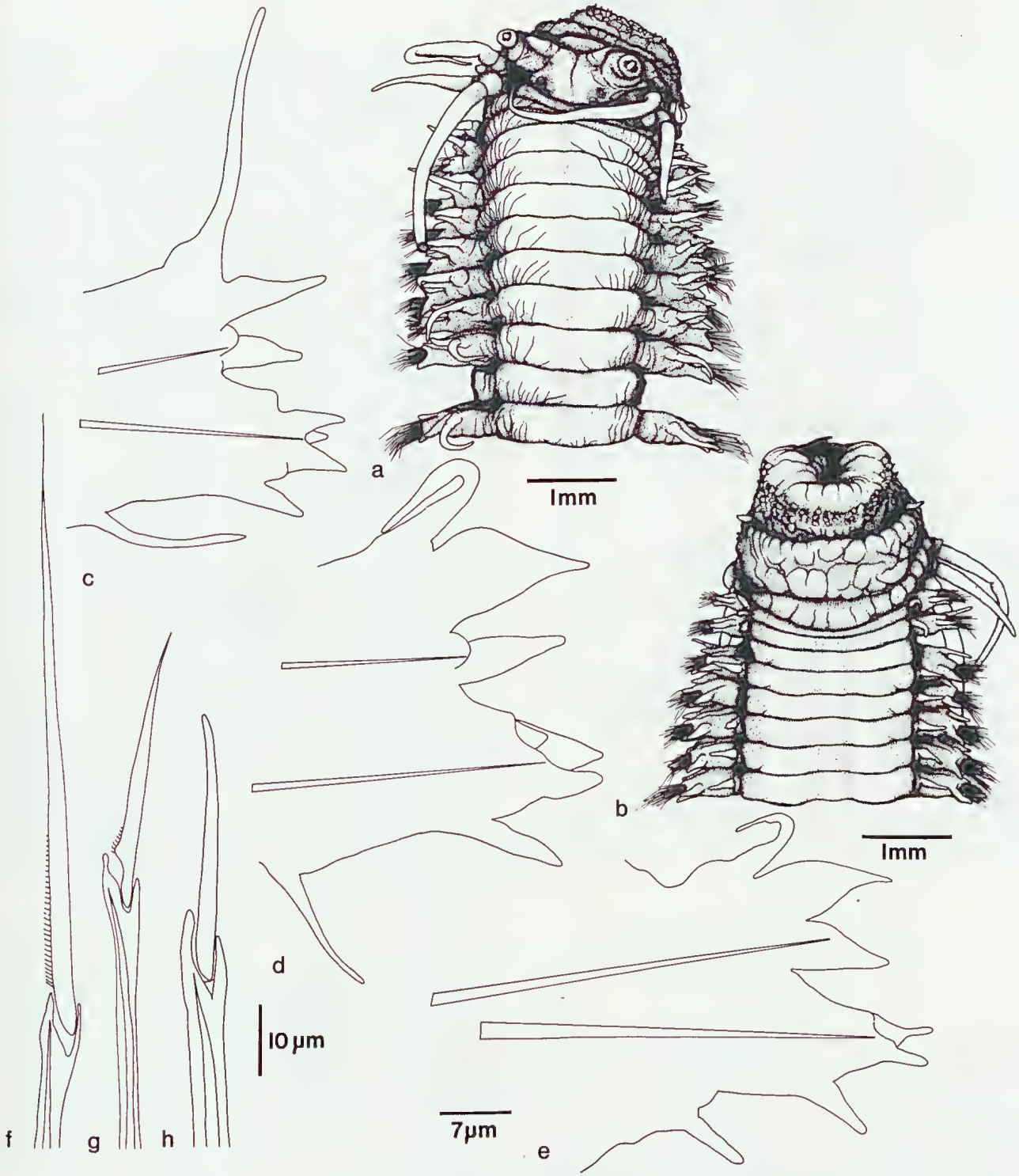


**Fig.1.** *Leonnates bolus* n.sp. Holotype: (a) anterior end, dorsal view; (b) anterior end ventral view; (c) parapodium 3, anterior view; (d) parapodium 20, anterior view; (e) parapodium 50, anterior view; (f) homogomph spiniger, parapodium 20 (neuropodium, supra-acicular fascicle); (g) heterogomph spiniger, parapodium 20 (neuropodium, subacicular fascicle); (h) paratype: (WAM 422-86), heterogomph falciger, parapodium 3 (neuropodium, subacicular fascicle).

spinigers in subacicular fascicle (Fig.1f-g). Subacicular fascicle of far anterior parapodia with 2 smooth, long-bladed heterogomph falcigers (Fig.1h). Spinigers of 2 types, long and short bladed. Spinigers in middle, anterior and ventralmost positions of subacicular fascicle short bladed.

**Variation.** Paratypes are pink-brown in colour. The following variation in paragnath and papillae counts is found:- maxillary ring paragnaths: Area I = 14-18, II = 12-14, III = 28-36, IV = 8-10; oral ring papillae: Area V = 0, VI = 2, VII-VIII = 8-9 (with 4 small and 4-5 large papillae). Maxillary ring paragnaths form continuous band with individual Areas not well defined. Neurosetae numerous. Falcigers present in the neuropodia of parapodia 3 of one paratype only. Falcigers not present in parapodia 10 of any paratypes. It appears that these falcigers are confined to far anterior setigers and are few in number.

**Remarks.** The species can be readily distinguished from other species of *Leonnates* in the unusual arrangement of pharyngeal papillae and paragnaths. The latter are arranged in two broad bands and the former composed of large blunt and small, sharply pointed papillae which are widely spaced. *Leonnates bolus* n.sp. can be distinguished from *L. decipiens* Fauvel, 1929 by the greater number of paragnaths occurring on Area III.

**Habitat.** Mangroves. The holotype (NTM W2518) was found inside mounds made by the burrowing lobster, *Thalassina squamifera* de Man. Specific habitat details for the paratypes are not available.

**Distribution.** Australia (Northern Australia, from Admiralty Gulf Western Australia 14°35'S 125°53'E to Darwin Harbour 12°30'S 130°55'E).

**Etymology.** The specific name *bolus* from the latin meaning 'lump of earth' refers to the *Thalassina* mound in which the holotype was found.

### *Leonnates crinitus* n.sp.

Fig.2a–g

**Material examined.** HOLOTYPE: Queensland, Cairns, Trinity Bay, 16°25'S 145°27'E, intertidal, 10 Dec. 1974, 1(QM GH4683), 62 mm long, 2.0 mm wide, 1.5 mm jaw length, 99 setigers, incomplete. PARATYPES: Queensland, Cairns, Trinity Bay, 16°25'S 145°27'E, intertidal, 10 Dec. 1974, 1(QM GH4684), (BMNH ZB1989.30), (USNM 123355). Paratypes range from 20-29 mm long, 2.0-2.2 mm wide, 1.8-2.0 mm jaw length, 33-47 setigers. All paratypes incomplete.

**Non-type material.** Northern Territory, Port Essington, Wangewanja Cove, 11°23'S 132°09'E, intertidal, 13 Sept. 1985, 1(NTM W3348); Cobourg Peninsula, Trepang Bay, 11°07'S 113°58'E, 5 m, 15 Sept. 1981, 3(NTM W00388). Queensland, Proserpine, 20°24'S 148°35'E, intertidal, (QM G10498); Moreton Bay, Bramble Bay, 27°25'S 153°20'E, 2.5 m, Dec. 1973 (QM GH4038). Specimens range in size up to 80 mm long, 3.2 mm wide, 2.7 mm jaw length, 146 setigers, complete.

**Description.** Colour in alcohol pink to pale brown. Anterior edge of prostomium with rust-brown pigmentation. Dorsal ligules with pale brown glandular areas, especially prominent in median and posterior parapodia. Prostomium trapezoidal, eyes round, of approximately equal size with distinct lenses. Palps long, cylindrical with long, digitiform palpostyles. Paired antennae extend slightly short of palps. Dorsalmost pair of tentacular cirri longest, extend to setiger 7 (Fig.2a). Jaws slender with straight cutting edge. Pharynx with paragnaths on maxillary ring arranged as follows: Area I = 1, II = 13, III = 40, IV = 19. Papillae on oral ring arranged as follows: V = 0, VI = 1 large rounded papillae, VII-VIII = 8 in single row.

Anterior notopodia with conical dorsal ligules, shorter, conical median ligules and superior lobes (Fig.2b-c). Dorsal cirrus narrow, tapering, slightly shorter than dorsal ligule. Neuropodia with subconical acicular lobe and longer, digitiform postsetal lobe. Ventral ligule subconical, equal to postsetal lobe in length. Ventral cirrus delicate, tapering, half as long as ventral ligule. Notopodial and neuropodial lobes approximately equal length. Median and posterior parapodia (Fig.2d) with notopodial superior lobe and neuropodial acicular and postsetal lobes greatly reduced. Dorsal ligules with prominent glandular areas.

Notopodia with homogomph spinigers; neuropodia with homogomph spinigers and falcigers in supra-acicular fascicle (Fig.2f), homogomph and sesquigomph spinigers and homogomph and sesquigomph falcigers in subacicular fascicle (Fig.2e,g). Falcigers in dorsalmost position of subacicular fascicle homogomph, ventralmost falcigers sesquigomph. Neuropodial supra-acicular falcigers first present from setiger 18. Falcigers with curved, digitiform distal tooth. Blades distally boldly serrated; proximally teeth long and fine.

**Variation.** Based on paratypes and non-type material examined. Specimen QM GH1048 has brown bands of pigment on dorsum and ventrum, most prominent anteriorly. Glandular regions of dorsal ligules are dark brown to black. This specimen is gravid. The species vary in paragnath and papillae counts: maxillary ring paragnaths - Area I = 1-4, II = 7-18, III = 25-40, IV = 13-22; oral ring papillae - Area V = 0, VI = 1, VII-VIII = 7-9. Neuropodial supra-acicular falcigers first present from setigers 16-18.

**Remarks.** *Leonnates crinitus* n.sp. is very similar to *Leonnates decipiens* Fauvel, 1929 in the shape of the parapodia and falciger blades but may be distinguished

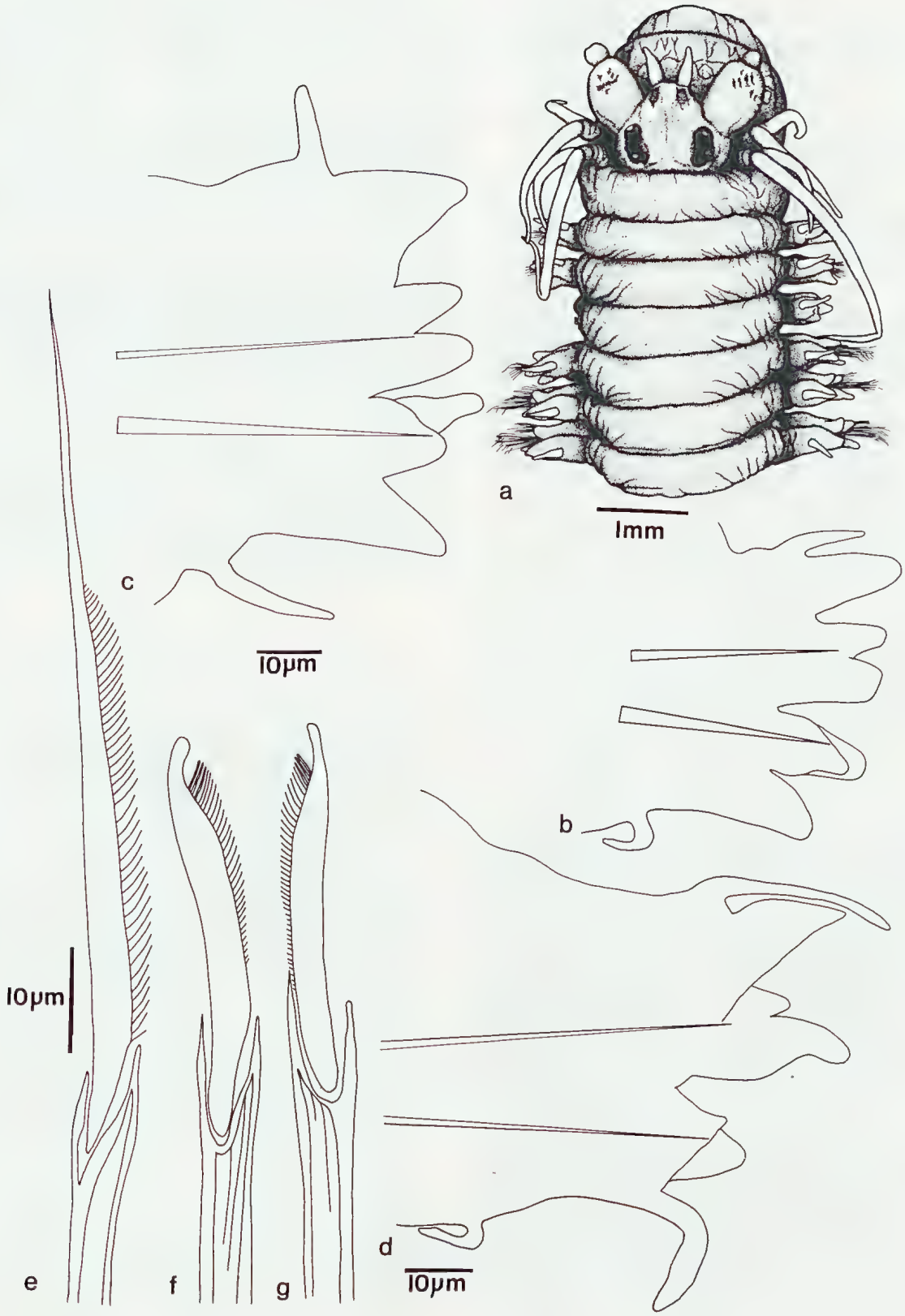


**Fig.2.** *Leonnates crinitus* n.sp. Holotype: (a) anterior end, dorsal view; (b) parapodium 3, anterior view; (c) parapodium 10, anterior view; (d) parapodium 50, anterior view; (e) sesquigomph spiniger, parapodium 10 (neuropodium, subacicular fascicle; (f) homogomph falciger, parapodium 20 (neuropodium, supra-acicular fascicle); (g) sesquigomph falciger, parapodium 20 (neuropodium, subacicular fascicle).

from *L. decipiens* by the presence of paragnaths in Area I. *Leonnates crinitus* n.sp. also has a greater number of paragnaths in Area III (25-40) than *L. decipiens* (6-16).

**Habitat.** Muddy sand, intertidal to 5 m, sometimes found inside rotting bark (NTM W3348).

**Distribution.** Australia (Northern Australia from Port Essington 11°23'S 13°'09'E to Moreton Bay 27°25'S 153°20'E).

**Etymology.** The specific latin name *crinitus* meaning long-haired or fringed refers to the long, fine falciger teeth on the distal portion of the blade seen in this species.

### *Leonnates decipiens* Fauvel

*Leonnates decipiens* Fauvel, 1929: 180-182, fig.1.–Fauvel, 1930: 20-21, fig.5f-m.–1953: 171-172, fig.87a-g.–Day, 1967: 330, fig.14.11n-s.

**Material examined.** Northern Territory, Black Rocks Landing, 15°53'S 136°35'E, 13 m, 29 Apr. 1982, 1(NTM W213); Table Headland, 11°13.5'S 132°20'E, 3-4 m, 4 May 1982, 2(NTM W231); Sandy Island, 11°10'S 132°09'E, 13 m, 29 Apr. 1982, 1(NTM W227); Port Bremner, Danger Point, 11°8.5'S 132°18.8'E, 6-7 m, 1 May 1982, 3(NTM W222).

**Description.** Largest specimen 4.5 mm long, 2.0 mm wide, 110 setigers, incomplete. Colour in alcohol cream-brown with prominent glands visible in dorsal ligules. Longest tentacular cirri extends to setiger 6. Jaws with smooth cutting edge. Maxillary ring of pharynx with paragnaths arranged as follows: Area I = 0, II = 1-9 (usually 5-9), III = 6-16, IV = 4-12. Oral ring with papillae arranged as follows: Area V = 0, VI = 1 large papilla, VII-VIII = 4-5 papillae in single row. Anterior notopodia with conical dorsal and median ligules and slightly shorter, conical superior lobe. Dorsal cirrus slightly exceeds length of dorsal ligule. Neuropodia with conical acicular and postsetal lobes. Ventral ligule subconical, exceeds length of acicular lobes. Short tapering ventral cirrus. In posterior parapodia, notopodial ligules exceed neuropodial ligules in length. Notopodial ligule elongate, broad based, glandular, exceeds length of median ligule. Acicular lobe elongate, digitiform; postsetal lobe shorter, conical; ventral ligule long, conical. Ventral cirrus as for anterior setigers.

Notosetae homogomph spinigers; neurosetae with homogomph and sesquigomph spinigers and heterogomph falcigers. From setiger 13, subacicular neuropodia with sesquigomph falcigers with blunt truncated tip and teeth on distal one half to one third of blade.

**Remarks.** Our material has fewer paragnaths in Areas VII-VIII than Fauvel's (1953) material, but it agrees well in other respects to previous descriptions. Two females (NTM W227 and NTM W222) were gravid with no sign of epitokal modification. This species can be distinguished from *Leonnates crinitus* n.sp. as *L. decipiens* Fauvel, 1929 has no paragnaths in Area I and fewer paragnaths in Area III than *L. crinitus* n.sp.

This is the first time that this species has been reported from Australian waters. Type material could not be examined as the Museum D'Histoire Naturelle, Paris has a policy of not lending type material. The original description by Fauvel (1929) is comprehensive and the Australian material closely fits this description except for the fewer paragnaths present in Areas VII to VIII, which we believe represent variation within the species.

**Habitat.** Australian material found among coral rubble and sandy substrata.

**Distribution.** Australia (Northern Territory from Black Rocks Landing 15°53'S 136°35'E to Port Bremner 11°07'S 132°20'E), Congo, Gulf of Mannar (type locality), Mozambique, Suez, Sri Lanka.

### *Leonnates jousseaumei* Gravier

*Leonnates jousseaumei* Gravier, 1899: 234-237, figs 1-5.–Gravier, 1901: 160-164, pl.11, figs 34-37.–Fauvel, 1919: 400.–Horst, 1924: 150.–Fauvel, 1930: 19, fig.5a-e.–Fauvel, 1931: 43-44, fig.4a.–Fauvel, 1932: 85.–Fauvel, 1953: 169-170, figs 86d-f.–Day, 1967: 330-331.

**Material examined.** Western Australia, Dampier Archipelago, Rosemary Island, 20°03'S 116°10'E, 64 m, 4 Dec. 1979, 1(WAM 166-86); Fenelon Island, 14°02'S 125°43'E, 6 m, 8 Feb. 1988 2(AM W202841). Northern Territory, McCluer Island, 11°05'S 133°01'E, 8-10 m, 17 Oct. 1989, 1(NTM W00445); Sandy Island, 11°07'S 132°17.5'E, 6-7 m, 22 Oct. 1981, 2(NTM W212). Queensland, Princess Charlotte Bay, 14°07'S 143°09'E, 12-15 m, 23 Feb. 1979, 1(AM W202842); Lizard Island, 14°40'S 145°28'E, 21 Dec. 1986, epitokes swimming at surface, 8(AM W203041), 2(AM W203042), 6 m, 2 Dec. 1985, 1(AM W203043); One Tree Island, 23°30'S 152°05'E, 31 m, 2 Nov. 1974, 1(AM W7257); Moreton Island, Tangalooma, 27°00'S 153°00'E, 10 m, 25 Nov. 1976, 1(QM GH3924).

**Description.** Material examined up to 70 mm long, 5.5 mm wide, 5 mm jaw length, 115 setigers. Colour in alcohol ranging from cream yellow to rust brown. Pharynx with paragnaths on maxillary ring arranged as follows: Area I = 0, II = 6-24, IV = 7-26. Area III = 3-10 paragnaths or papillae. Oral ring with papillae arranged as follows: Area V = 0, VI = 6-16, VII-VIII = 20-72 in 2-3 irregular rows. Longest tentacular cirri extends to setiger 6. Notopodia with dorsal cirri slightly longer than dorsal ligule, 3 conical, pointed, notopodial

ligules. Long, slender superior lobe slightly reduced in posterior setigers. Neuropodia with conical, acicular and slightly longer postsetal lobes, large, conical, ventral ligule and shorter ventral cirrus. These lobes are reduced posteriorly.

Notopodia with homogomph spinigers throughout, and few homogomph falcigers in far posterior setigers. Neuropodia with spinigers and falcigers. Falcigers with boldly serrated blades, distally curved with a pointed terminal tooth.

**Variation.** Some specimens, AM W20284 and the Lizard Island epitokes (AM W203041, AM W203042, AM W203043) have dark bands of brown pigmentation on the prostomium, peristomium and on a few anterior setigers. Epitokes also have a longitudinal band of brown pigmentation on the modified end of body. One female (AM W202841) is gravid with no sign of epitoky. Male epitokes collected in October/November showed modification of parapodial lobes and setae from setiger 12 onwards. The papillae present on Area III and sometimes Area IV are sclerotised to varying degrees. In some specimens (especially smaller ones) there is no evidence of sclerotisation, others are partially but none are fully sclerotised.

**Remarks.** Partial sclerotisation of the pharangeal papillae has also been noted by Fauvel (1919) and Horst (1924). This species is very similar to *Leonnates nipponicus* (Imajima, 1972). From Imajima's description it appears that *L. jousseaumei* differs from *L. nipponicus* which has no notopodial falcigers in posterior setigers, no paragnaths in Area III and greater reduction of the notopodial superior lobe. This is the first record of the species from Australian waters, but it has already been reported from the Indo-Pacific. Type material is not available for loan from the Museum D'Histoire Naturelle, Paris, but Gravier's original description is expansive and our material agrees well with the original description.

**Habitat.** The Australian material was generally found amongst coral debris in 6 to 64 m. Two specimens (NTM W00445, AM W7257) were found inside sponge tissue in holes closely approximating the shape and size of the worm.

**Distribution.** Australia (Northern Australia from Rosemary Island Western Australia 20°03'S 116°10'E to Moreton Island, Queensland 27°00'S 153°00'E), Red Sea, Malay Peninsula, Madagascar, Indonesia, India, Gulf of Manna Pambam, Pakistan.

### *Leonnates stephensoni* Rullier

*Leonnates stephensoni* Rullier, 1965: 174-177, fig.4A-I.–Hutchings & Murray, 1984: 36-37, fig.11.

**Material examined.** HOLOTYPE: Queensland, Moreton Bay, 27°25'S 153°20'E, 10 Feb. 1961, 1(AM W3790). Western Australia, Cockburn Sound, 32°11'S 115°43'E, 4 Aug. 1970, 2(WAM 516-86). Northern Territory, McArthur River, Black Rocks Landing, 15°53'S 136°35'E, 1 Aug. 1985, 1(NTM W3480); McArthur River, Curie Channel, 15°47'S 136°40'E, 7 Aug. 1985, 1(NTM W3111), 7 Aug. 1985, 1(NTM W3165), 7 Aug. 1985, 1(NTM W3174), 7 Aug. 1985, 1(NTM W3500). Queensland, Halifax Bay, 19°10'S 146°44'E, Jan. 1977, (AM W202000), 19°10'S 146°38'E, 5 m, Jan. 1977 (AM W202002), 10°10'S 146°37'E, 2 m, Jan. 1977 (AM W202003), 19°07'S 146°33'E, 2 m, (AM 202005); Shoalwater Bay, Triangular Island, 22°23'S 150°30'E, 1981-1982, 2(AM W202843); Auckland Creek, 23°50'S 151°16'E, 9 Feb. 1976, 1(AM W10258), Aug. 1988, 1(AM W13190); Gladstone Harbour, 23°51'S 151°16'E, 6 Nov. 1975 (QM G10536), 6 Nov. 1975 (QM G10538), 6 Nov. 1975 (QM G10541), 6 Nov. 1975 (QM G10542); Calliope River, 23°55'S 151°10'E, May 1976, 4(AM W13513), June 1976, 10+(AM W13515); Middle Bank, 25°47'S 153°07'E, 10 m, 13 Dec. 1962 (QM G4873); Moreton Island, 27°11'S 153°24'E, 15.3 m, 14 Dec. 1962 (QM G4874); Moreton Bay, 27°25'S 153°20'E, 27 m, Sept. 1972 (QM G10371), 7.6 m, Mar. 1970 (QM G10452), 33.5 m, Sept. 1972 (QM G12691); Brisbane River, 27°28'S 153°02'E, 19 Sept. 1975 (QM GH3980), 10 Apr. 1975 (QM GH3978); Peel Island, 6.4 m, Sept. 1971 (QM G10354), 9.5 m, June 1970 (QM G10365). New South Wales, Lake Macquarie, 32°59'S 151°38'E, Feb. 1979, 1(AM W17832), Jan. 1978, 1(AM W197749); Hawkesbury River, 33°33'S 151°16'E, 10 m, 7 May 1979, 1(AM W196446), 1(AM W196447).

**Description.** Material examined up to 40 mm long, 5.0 mm wide, 0.25-2.0 mm jaw length. Colour in alcohol cream-pale brown, often with conspicuous brownish glands in dorsal cirri and notopodial dorsal ligules. Dorsalmost pair of tentacular cirri longest extending up to setiger 12, remaining pairs shorter. Anterior pair of eyes reniform, posterior pair spherical. Jaws slightly crenulated on the cutting edge, without distinct teeth. Maxillary ring of pharynx with paragnaths arranged as follows: Area I = 0, II = 2, III = 0, IV = 2-3. Oral ring with papillae as follows: Area V = 3 small papillae, VI = 2 papillae, VII-VIII = approximately 20-33 irregularly arranged papillae.

Anterior notopodia with digitiform superior lobe, broad based, conical dorsal ligule, conical median ligule and slightly shorter, conical superior lobe. Neuropodia with conical acicular and postsetal lobes, acicular lobe projecting ventrally, postsetal lobe projecting dorsally. Postsetal lobe slightly longer than ventral ligule. Ventral cirrus slightly shorter than ventral ligule. In median and posterior parapodia, dorsal ligule expanded, notopodial superior lobe reduced. Ventral ligule exceeds acicular and postsetal lobes in length. Ventral cirrus narrow, tapering.

Notopodia with homogomph spinigers throughout. Neuropodia with homogomph spinigers and falcigers in supra-acicular fascicle, homogomph falcigers in subacicular fascicle. Falcigers long bladed, strongly denticulate with terminal rectangular projection.

**Habitat.** Sandy mud.

**Distribution.** Australia (widespread north of 30°S; from Western Australia, Cockburn Sound, 32°11'S 115°43'E to New South Wales, Hawkesbury River, 33°33'S 151°16'E).

### *Platynereis* Kinberg

*Platynereis* Kinberg, 1866: 177.–Wilson, 1985: 136.

**Type species.** *Platynereis magalhaensis* Kinberg, 1866, by original designation.

**Diagnosis.** Prostomium with 2 antennae, 1 pair of biarticulate palps and 2 pairs of eyes. Pharynx with paragnaths on both rings, including cones and pectinate bars. Four pairs of tentacular cirri, parapodia biramous. Notosetae homogomph spinigers and falcigers. Falcigers sometimes simple. Neurosetae homogomph and heterogomph spinigers and heterogomph falcigers.

**Remarks.** Fauchald (1977) indicates that 20 species have been described, and no revision of the genus has been undertaken.

### Key to Australian Species of *Platynereis*

1. Notopodial falcigers first present from setigers 3-5. Pectinate bars on oral ring long, in a single row ..... *Platynereis uniseris* n.sp.

—— Notopodial falcigers first present after setiger 12. Pectinate bars on oral ring usually in 2-3 short rows ..... 2

2. Simple, bifid notopodial falcigers present from setigers 12-13 ..... *Platynereis bicanaliculata*

—— Simple falcigers absent ..... 3

3. Notopodial falcigers absent in adults. Dorsal cirri and notopodial dorsal ligules elongate posteriorly ..... *Platynereis australis*

—— Notopodial falcigers present posteriorly. Dorsal cirri and notopodial dorsal ligules not markedly elongate posteriorly ..... 4

4. Notopodial falcigers present posteriorly, usually from setiger 22 ..... *Platynereis dumerilii antipoda*

—— Notopodial falcigers posteriorly, from setigers 14-17 ..... *Platynereis polyscalma*

### *Platynereis australis* (Schmarda)

*Heteronereis australis* Schmarda, 1861: 101-102, pl.31, fig.242.
*Platynereis magalhaensis* Kinberg, 1866: 177.–Hartman, 1954: 36.
*Platynereis australis*.–Knox 1951: 223-225, pl.49, figs 34-40.–Hartmann-Schröder, 1962: 427.-Day, 1967: 305, fig.14.4m.–Knox & Cameron, 1971: 28.–Imajima, 1972: 82-85, figs 21a-o, 22.

**Material examined.** New South Wales, Newport, 33°39'S 151°19'E, 10-12 m, 1(AM W202879); Long Reef, 33°45'S 151°19'E, 4(AM W4323); Manly, 33°48'S 151°17'E, 20 Jan. 1968, 1(AM W4321); Port Jackson, 33°50'S 151°17'E, 20(AM W4854) 20(AM W4855); Coogee, 31°29'S 142°12'E, Dec. 1921, 1(AM W4796); Merimbula, 36°54'S 149°54'E, 35 m, 16 Mar.1976, 1(AM W15761); Jervis Bay, Green Patch, 34°48'S 153°24'E, 20-30 m, 28 Feb. 1976, 1(AM W202881), Summer Cloud Bay, 30-50 m, 29 Nov. 1971, 5+(AM W202884); Twofold Bay, Munganno Point, 37°06'S 149°56'E, 3 m, 3(AM W202880). Western Australia, Cockburn Sound, 32°11'S 115°43'E, 2-3 m, 13 Feb. 1972, 2(WAM 51-72).

**Description.** Similar to *Platynereis dumerilii antipoda* in all respects except notopodial falcigers absent in adults and posterior dorsal cirri and notopodial dorsal ligules longer in *P. australis.*

**Remarks.** Type material has not been examined and has not been located in any major institution. Also no material is available from the type locality. The above specimens were all posteriorly complete, with posteriorly enlarged dorsal ligules and without notopodial falcigers. All specimens were large and presumably mature. The very close similarity between this species and *P. dumerilii antipoda* and the difficulty in distinguishing posteriorly incomplete specimens suggest that a detailed examination of these two species is needed to seek further distinguishing characters.

**Habitat.** Intertidal under rocks, algal holdfasts.

**Distribution.** Australia (eastern Australia from Newport 33°29'S 151°19'E to Twofold Bay 37°06'S 149°56'E). One specimen from Cockburn Sound, Western Australia. New Zealand, Auckland (type locality).

### *Platynereis bicanaliculata* (Baird)

*Nereis bicanaliculata* Baird, 1863: 109.
*Nereis Agassizi* Ehlers, 1868: 542-546 pl.23, fig.1.–Izuka, 1912: 160-162, pl.1 fig.9, pl.17 figs 9-11.
*Nereis Platynereis Agassizi.*–Augener, 1927: 140-141.
*Nereis dumerilii* Marenzeller, 1879: 123-125, pl.2 fig.4A,B.
*Nereis Dumerilii.*–Izuka, 1912: 158-160, pl.17 figs 7,8.
*Nereis (Platynereis) kobiensis* McIntosh, 1885: 210-212, pl.34 figs 3-6; pl.16a figs 2-4.
*Nereis kobiensis.*–Izuka, 1912: 162-163, pl.17 figs 12,13.
*Platynereis agassizi.*–Fauvel, 1936: 64-65.–Okuda, 1938: 93.–Okuda & Yamada, 1954: 185-186, fig.3G.
*Platynereis bicanaliculata.*–Hartman, 1954: 36-39, figs 38,39.–Imajima & Hartman, 1964: 152-153.–Wu, 1967: 57-58, fig.5a-b.–Imajima, 1972: 76-79, figs 18A-M, 19A-E, 22.–Hutchings & Murray, 1984: 42.

**Material examined.** New South Wales, Port Stephens, Nelson Bay, 32°44'S 152°09'E, 27 July 1976, 1(AM W12586), 22 July 1976, 1(AW W12626), 27 July 1976, 1(AM W197870); Port Jackson, 33°50'S 151°17'E, Feb. 1910, 2(AM W68), Feb. 1910, 1(AM W70); Rose Bay, 33°52'S 151°16'E, Feb. 1910, 1(AM W85); Botany Bay, 34°00'S 151°11'E, 17 Jan. 1975, 1(AM W19033); Kurnell, 34°00'S 151°13'E, 25 May 1975, (AM W7952); Jervis Bay, Green Patch, 34°48'S 153°24'E, 1(AM W202828). South Australia, Flinders Island, 33°40.5'S 134°22.0'E, 17 m, 19 Apr. 1985, 7(MV F56465). Western Australia, Nornalup, 35°00'S 116°44'E, Sept. 1973, 3+(WAM 101-84).

**Description.** Tentacular cirri slender, longest extending to setiger 10. Jaws, heavily sclerotised with 6-7 teeth. Pharynx with short pectinate bars arranged as follows: Area I = 0, II = 0, III = an oval patch, IV = conical group of short pectinate bars, V = 0, VI = 2-3 transverse rows of pectinate bars, Areas VII-VIII = 5 double transverse rows of pectinate bars. Parapodial lobes are conical anteriorly, conical posteriorly with dorsal cirri exceeding length of dorsal ligules throughout.

Notopodia with homogomph spinigers and 1-3 dark-brown simple falcigers from setiger 12-13. Falcigers bifid with hooked tips and distinct tendon. Neuropodia with homogomph spinigers and short-bladed heterogomph falcigers in supra-acicular fascicle and heterogomph spinigers and falcigers in subacicular fascicle.

**Habitat.** The Australian material was collected from under rocks, in sand, among kelp holdfasts, among calcareous algae, and among seagrasses *Zostera* and *Halophila.*

**Distribution.** Australia (south-eastern to south-western Australia from Port Stephens 32°44'S 152°09'E to Nornalup, Western Australia 35°00'S 116°44'E), Western Canada, Esquimalt Harbour, Vancouver (type locality) to Western Mexico, Hawaii, Japan, Taiwan.

### *Platynereis dumerilii antipoda* Hartman

*Platynereis dumerilii antipoda* Hartman, 1954: 35-36, fig.33-37.–Russell, 1962: 5.–Hartmann-Schröder, 1979: 118.–Hartmann-Schröder, 1987: 49.–Hutchings & Rainer, 1979: 757-758.–Hutchings & Turvey, 1982: 141.–Wilson, 1985: 136-137.

**Material examined.** Queensland, Hervey Bay, Pialba, 25°17'S 152°50'E, 30 Mar. 1972, 2(AM W202898). New South Wales, Nambucca Heads, 30°39'S 153°01'E, 6 Jan. 1969, 1(AM W4850); Port Stephens, 32°34'S 152°09'E, 3(AM W4848), 27 July 1976, 1(AM W12432), 27 July 1976, 2(AM W12473); Lake Macquarie, 32°59'S 151°38'E, 31 Mar. 1971, many(AM W4722), 13 Sept. 1954, 1(AM W4849), 18 Sept. 1953, 1(AM W4853); Long Reef, 33°45'S 151°19'E, 19 Jan. 1968, 2(AM W4323), 6 Nov. 1922, 1(AM W4852); Middle Head, 33°33'S 151°18'E, 19 Dec. 1968, 10(AW W4851); Gunnamatta Bay, 34°05'S 151°09'E (QM G4094); Jervis Bay, Murrays Beach, 35°03'S 150°44'E, 25 Apr. 1972, 1(AM W194159), 17 Oct. 1972, 3(AM W194490); Merimbula, 36°54'S 149°54'E, 13 Dec. 1975, 1(AM W15776), 17 Feb. 1976, 1(AM W15777), 24 July 1975, 1(AM W15778). Tasmania, Bellerive, 42°52'S 147°22'E, Jan. 1979, 1(TASM K1002); Hobart, 42°53'S 147°19'E, 20 Feb. 1909, 1(TASM K1001); Bruny Cape, 43°30'S 147°09'E, 30 Mar. 1964, 1(AM W18183). South Australia, Encounter Bay, 35°35'S 138°45'E, 18 July 1988 8(AM W202823); Port Willunga, 35°16'S 138°28'E (SAM E2374); Sellicks Beach, 35°20'S 138°27'E, 16 Mar. 1979, 1(AM W18319); Kangaroo Island, 35°40'S 137°05'E, 5 Mar. 1989, many(AM W18325); Waldegrove Island, 33°36'S 134°37'E, 16 Mar. 1979, 1(AM W18319), St Francis Island, 32°31'S 133°18'E (SAM E312), (SAM E2375); West Island, 32°31'S 133°15'E (SAM E2376). Western Australia,

Rottnest Island, 32°00'S 115°30'E, 29 Nov. 1945, 3(AM W5708), 28 Nov. 1945, 20(AM W5721), 1-2 m, 30 June 1972, 4(WAM 67-72); Cockburn Sound, Woodman Point, 32°11'S 115°43'E, 20 Feb. 1972, 3+(WAM 505-86), 28 Feb. 1978, 3+(WAM 507-86), Sept. 1972, 3+(WAM 522-86); Carnarvon, 24°53'S 113°40'E, 17 June 1972, 1(AM W5473).

**Description.** Material examined up to 30 mm long, 1.5 mm wide, 0.4-2.0 mm jaw length. Colour in alcohol, cream. Prostomium trapezoidal. Eyes with distinct lenses. Palps globular with rounded palpostyles. Dorsalmost pair of tentacular cirri longest extend up to setiger 12. Jaws robust with up to 9 teeth. Pharynx with pectinate bars arranged as follows: Area I = 0, II = 0, III = up to 3 groups of short bars, IV = 4-12 bars in up to 8 rows (often incomplete particularly toward the maxillary edge), V = 0, VI = 2-3 short bars, VII-VIII = 5 transverse groups in 2-3 rows (usually 2).

Anterior notopodia dome shaped in far anterior setigers, subconical from approximately setiger 10 onwards. Dorsal and median ligules of approximately equal length with small superior lobe. Dorsal cirri long, exceed length of dorsal ligule. Neuropodia with conical acicular and shorter conical postsetal lobe. Ventral ligule conical, slightly shorter than median ligule. Ventral cirrus slender, tapering, slightly shorter than ventral ligule. Posteriorly, dorsal ligule expanded, glandular at base, exceeds median ligule in length. Neuropodial acicular and postsetal lobes greatly reduced. Lobes digitiform rather than conical in shape.

Notopodia with homogomph spinigers throughout. Homogomph falcigers present midposteriorly, sometimes present from setiger 22, usually present from setiger 25-30 though extremely variable. Neuropodia with homogomph spinigers and heterogomph falcigers in the supra-acicular fascicle, heterogomph spinigers and falcigers in the subacicular fascicle. Notopodial falcigers long bladed, curved distally, sometimes with distal notch.

Live specimens (AM W202823) were pale green with red speckling on body; palps and cirri whitish; and orange around the eyes.

**Remarks.** As previously mentioned by Wilson (1985) the position at which notopodial falcigers first appear is variable and does not appear to be size related. This species is closest to *P. polyscalma* Chamberlin, 1919 but can be distinguished from it by the position at which notopodial falcigers are first present (usually at setigers 14-17 in *P. polyscalma* Chamberlin, 1919). A detailed examination of *Platynereis dumerilii* and its subspecies is needed to determine whether the subspecific status of the Australian and New Zealand *P. dumerilii antipoda* is justified or if it should be raised to full specific status. The differences between *Platynereis dumerilii* Audouin & Milne-Edwards, 1834, a cosmopolitan warm temperate species, and *P. dumerilii antipoda* Hartman, 1954 are largely qualitative and until a thorough revision of *P. dumerilii* is undertaken, it is not possible to ascertain whether these differences are due to ecophenotypic or genotypic effects. A revision should also include the closely related species, *Platynereis australis* Schmarda, 1861, whose status needs to be verified.

**Habitat.** Australian specimens are usually associated with algae, seagrass or encrusting fauna such as bryozoans. Substrate generally muddy sand, and intertidal, though material has been collected to depths of 95 m (Wilson, 1985).

**Distribution.** Australia (south-eastern to south-western Australia from Nambucca Heads, New South Wales 30°39'S 153°01'E to Cape Peron, Western Australia 25°30'S 113°31'E), New Zealand. Russell (1962) recorded this species from Dunwich, south-east Queensland (27°30'S 153°24').

### *Platynereis polyscalma* Chamberlin

*Platynereis polyscalma* Chamberlin, 1919: 219-226, pl.30 figs 5-8, pl.31 figs 1-10, pl.32 figs 1,2.–Monro, 1931a: 18.–Fauvel, 1932: 114-116.–Gravier & Danton, 1934: 117-123, figs 114-124.–Hartman, 1940: 229-231, pl.38 figs 76-83.–Fauvel, 1953: 221-222, fig.112a-e.–Reish, 1968: 217-218.

*Nereis (Platynereis) integer* Treadwell, 1920: 595-597, figs 1-4.

*Nereis (Ptatynereis) [sic] polyscalma.*–Horst, 1924: 186-187.

**Material examined.** Western Australia: Cockburn Sound, 32°11'S 115°43'E, 28 Feb. 1978, 1(WAM 514-86); Kalbarri, 27°42'S 114°12'E, 1.5 m, 9 Jan. 1984, 4(AM W202831); Broome, Mangrove Point, 17°58.5'S 122°14.5'E, 28 Sept. 1984, 1(NTM W2139); Heywood Island, 15°20'S 124°20'E, 10 July 1988, 12(AM W202971). Northern Territory: Darwin, Casuarina Beach, 12°20.6'S 130°52.6'E, 9 Oct. 1973, many(NTM W1389); Nightcliff, 12°22.5'S 130°51'E, 0.5 m, 9 Sept. 1975, 4(NTM W240); Coral Bay, 11°11'S 132°03'E, 2-5 m, 16 May 1983, 10(NTM W00402); Port Bremner, Danger Point, 11°7.5'S 132°20'E, 1-2 m, 1 May 1982, 12(NTM W233); Oxley Island, 11°00'S 132°48.5'E, 15 m, 21 Oct. 1982, 1(NTM W00427). Queensland: Thursday Island, Torres Strait, 10°35'S 142°13'E, 29 June 1976, 2(AM W202892); False Orford Ness, 11°23'S 142°52'E, 3-4 m, 18 Dec. 1979, 1(AM W202833); Raine Island, 11°43'S 144°03'E, 2-8 m, 11 Feb. 1979, 2(AM W202834); Yonge Reef, 14°37'S 145°35'E, 25 m, 2(AM W202893); Lizard Island, Chinamen's Head, 14°40'S 145°27'E, Jan. 1976, 1(AM W202838); Cairns, 16°36'S 146°15'E, 201-110 m, 14 Oct. 1981, 1(AM W202837); Low Isles, 16°23'S 145°34'E, surface, Oct. 1931, 1(AM W2950); Townsville, Pallarenda Beach, 19°16'S 146°49'E, 7 Feb. 1978, 1(AM W18109); Hervey Bay, Point Vernon, 25°06'S 152°49'E, 5-15 m, 31 Apr. 1977 1(AM W202835); Triangular Island, Shoalwater Bay, 22°23'S 150°30'E, 1(AM W202895); Heron Island, 23°27'S 151°55'E, 22 July 1975, (QM GH3979), 1(AM W202830),

1(AM W202832); Wistari Reef, 23°29'S 151°53'E, 36 m, 1(AM W197107); Gladstone, 23°51'S 151°16'E, 6 Nov. 1975, (QM GH4003), (QM GH4015), 1974-1983, 1(AM W199347), 1(AM W199349); Caloundra, 26°48'S 153°08'E, 29 Mar. 1972, 1(AM W202894); Moreton Bay, 27°25'S 153°20'E, 1(WAM 16-85).

**Description.** Material examined up to 40 mm long, 2.0 mm wide, 0.35-2.5 mm jaw length. Tentacular cirri long and slender, longest extending to setiger 20. Jaws pale golden with darker brown cutting edge. Pharynx with the following arrangement of paragnaths: Areas I = 0, II = 0, III = up to 10 patches of pectinae in 2-4 rows, IV = crescentric area of 5-10 patches of pectinae in 3 or 4 rows, V = 0, VI = 2 curved rows of pectinae, the row closest to the maxillary ring shortest, VII and VIII = transverse series of 5 short patches.

Parapodial lobes all conical with exception of conical ventral ligule. Dorsal cirri exceed length of dorsal ligules. Notopodia with homogomph spinigers and falcigers. Homogomph falcigers initially present from setigers 12-22 (usually from setigers 14-17) and continue along entire length. Falciger blade terminally smooth with a minute boss. Distinct tendon extends from tip of hooked falciger blade to upper one third of blade, below which are fine teeth. Articulation of shaft and blade of this falciger very obvious. Homogomph spinigers decrease in number posteriorly. Neuropodia with heterogomph spinigers and falcigers. Falciger blades short, recurved.

Female epitokes with parapodial lobes modified from setiger 20 onwards, male epitokes modified from setiger 15 onwards.

**Remarks.** Material agrees well with Hartman's (1940) description of atokous specimens from Cape San Lucas and La Paz Bay, California and San Lorenzo Channel, Espiritu Santo Island. Epitokes agree well with Chamberlin's original description.

**Habitat.** Australian material was collected amongst coral rock, weed, sand and mud and often associated with brown algae and *Halimeda*.

**Distribution.** Australia (north-western to north-eastern Australia in tropical to warm temperate waters, from Kalbarri, Western Australia 27°42'S 114°12'E to Moreton Bay, Queensland 27°25'S 153°20'E), widely distributed in the tropical Pacific and Indian Oceans. Type locality Funafuti Atoll, Ellice Island.

### *Platynereis uniseris* n.sp.

Fig.3a–j

**Material examined.** HOLOTYPE: Western Australia: Ningaloo, 22°42'S 113°40'E (AM W202882), 14 mm long, 1.1 mm wide, 0.75 mm jaw length, 54 setigers. PARATYPES: Western Australia: Ningaloo, 22°42'S 113°40'E, 2 Jan. 1974, 1(AM W202883), 1(AM W202884), 1(AHF POLY1495), 1(BMNH ZB1989.31), 1(NTM W 5356), 1(USNM 127643). Paratypes range from 14-16.5 mm long, 1.0-1.3 mm wide, 0.75-0.9 mm jaw length, 55-73 setigers. All type material complete.

**Non-type material.** Western Australia: Cape Peron, 25°30'S 113°31'E, 1(AM W203044); Point Quobba, 24°29'S 113°25'E, 7 Jan. 1984, 10(AM W202866); Ningaloo, 22°42'S 113°40'E, 2 Jan. 1974, 25(AM W202861), 3 m, 31 Dec. 1973, 15(AM W202886), 2 m, 1 Jan. 1984, 3(AM W202887); Cape Range National Park, Neds Camp, 21°58'S 114°02'E, 12 m, 2 Jan. 1984, 5(AM W202863), 2 m, 31 Dec. 1983, 10(AM W202864); North West Cape, Mangrove Passage, 21°33'S 115°21'E, July 1980, 3+(WAM 500-86); Dampier Archipelago, Kendrew Island, 20°29'S 116°32'E, 14 Oct. 1973, 1(WAM 117-75); Dampier Archipelago, Hungerford Bay, Rosemary Island, 20°29'S 116°35'E, 6 m, 1 Apr. 1987, 1(AM W202891), 14 Oct. 1973, 1(WAM 144-75), 28 Oct. 1973, 1(WAM 169-75); Kimberleys, Condillac Island, 14°06'S 125°33'E, 6 m, 16 July 1988, 1(AM W203003); Cassini Island, 13°57'S 125°37'E, 18 July 1988, (AM W203004). Northern Territory: Trepang Bay, 11°10'S 131°58'E, 16 Oct. 1981, 1(NTM W236). Queensland: Raine Island, 11°39'S 144°08'E, 1-2 m, 10 Feb. 1979, 2(AM W202885), 2-20 m, 13 Feb. 1979, 1(AM W202888); Yonge Reef, 14°37'S 145°38'E, Jan. 1975, 1(AM W202849), 13 Jan. 1985, 1(AM W202850), Jan. 1975, 2(AM W202859), Jan. 1975, 1(AM W202862); Lizard Island, 14°37'S 145°38'E, 28 Feb. 1974, 3(AM W202847); Heron Island, 23°27'S 151°55'E, 29 Sept. 1984 (QM GH3917); Herald Group, Northeast Cay, 22°07'S 152°17'E, 9 Nov. 1964, 2(AM W202848); Currumbin Beach, 28°08'S 153°29'E, Jan. 1985 (QM GH 3918). New South Wales: Collaroy Beach, 32°06'S 150°07'E, 28 Feb. 1974, 3(AM W202847). Unless otherwise specified, specimens collected intertidally.

**Description.** Material ranges in size up to 25 mm long, 3.4 mm wide with jaw length of 2.5 mm for 77 setigers. Cream-yellow in alcohol with faint brown pigmentation on prostomium. Light brown glandular patches on dorsal ligules and dorsolateral edge of setigers, especially prominent posteriorly. Prostomium ovoid with 2 pairs equal-sized round, black eyes with distinct lenses (Fig.3a). Palps globular with large round palpostyles. Antennae conical, slightly shorter than prostomium. Tentacular cirri blunt-tipped, dorsalmost pair longest extends to setiger 5. Jaws large, strongly curved, translucent brown with 6 large teeth. Pharynx with pectinate bars on maxillary ring arranged as follows: Area I = 0, II = 0, III = 8 short bars with 1 row on each edge closest to Area IV and 3 parallel rows of 2 bars each ventrally, Area IV = 3 straight bars in conical arrangement, basal row broken plus an indistinct, short 4th row on edge closest to jaws; oral ring: Area V = 0, VI = 1 long very slightly curved bar, VII-VIII = 5 long bars. Anterior parapodia with dorsal cirrus narrow, tapering, greatly exceeds length of dorsal ligule. Notopodia with dorsal and median ligules dome shaped from setigers 3-8 (Fig.3b), subconical after approximately setiger 8 (Fig.3c). Neuropodia with conical acicular and slightly shorter

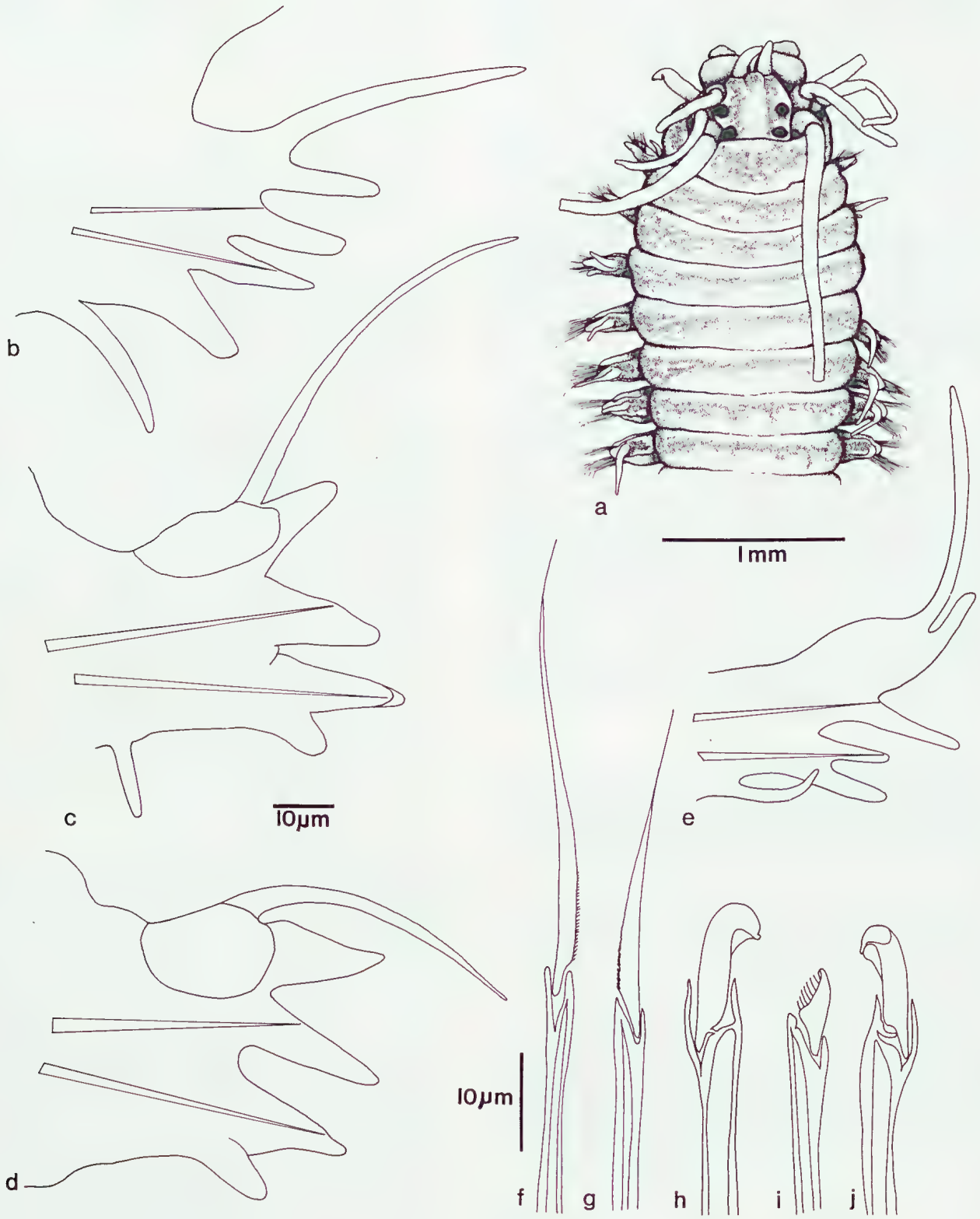


**Fig.3.** *Platynereis uniseris* n.sp. Holotype: (a) anterior end, dorsal view; (b) parapodium 3, anterior view; (c) parapodium 10, anterior view; (d) parapodium 20, anterior view; (e) parapodium 50, anterior view; (f) homogomph spiniger, parapodium 20 (neuropodium, supra-acicular fascicle); (g) heterogomph spiniger, parapodium 20 (neuropodium, subacicular fascicle); (h) homogomph falciger, parapodium 20 (notopodium); (i) heterogomph falciger, parapodium 20 (neuropodium, subacicular fascicle); (j) homogomph falciger, parapodium 50 (notopodium).

postsetal lobe. Ventral ligule, as for notopodial ligules, dome shaped in far anterior setigers (Fig.3c) then subconical (Fig.3d). Ventral cirrus one half to two thirds as long as ventral ligule. Notopodial lobes exceed neuropodial lobes in length. Posterior parapodia with lobes subconical in shape. Dorsal ligule exceeds length of median ligule in far posterior setigers and becomes swollen at its base otherwise similar to notopodia (Fig.3e).

Notopodia with homogomph spinigers and 1-2 homogomph falcigers after setiger 4. Neuropodia with homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph spinigers and heterogomph falcigers in subacicular fascicle (Fig.3f-j).

Spinigers all short bladed with coarse teeth at base of blade. Notopodial falcigers strongly curved with a slightly hooked tip connected to a distinct tendon. Articulation of shaft and blade strongly marked.

**Variation.** Some specimens have brown pigmentation on prostomium and dorsum of anterior setigers. Tentacular cirri extend from setigers 7-13. Range in number of pectinate bars varies as follows: Area I = 0, II = 0, III = 4-7 short bars, IV = 4-7 (some partially broken bars), V = 0, VI = 1, VII-VIII = 1-6.

Notopodial falcigers first present from setigers 3-5 (usually 4). Specimen lots AM W202864 and QM GH3917 are female epitokes with modification of parapodia and setae from setiger 21 onwards. A male epitoke, AM W202886, is modified from setiger 15 onward, and dorsal cirri on setigers 1-7 are greatly enlarged.

**Remarks.** This species is close to *P. calodonta* Kinberg, 1866, in the shape of the parapodia and in having notopodial falcigers, first present from the 4th or 5th setiger. However *P. uniseris* n.sp. can be distinguished from *P. calodonta* and other *Platynereis* species by the presence of a single row of long, pectinate bars in the oral ring. Comparison with the holotype of *Platynereis calodonta* (SSM 583) and specimens figured by Day (1934:fig.9b; 1967:figs 14.4e,f) showed the pectinate bars to be quite different. Pectinae in the holotype of *P. calodonta* are long toothed and in the form of discrete clusters, randomly arranged, not in distinct rows as in *Platynereis uniseris* n.sp., and bars are arranged in 2-3 rows in Areas VI to VIII in *P. calodonta*. Falciger blades of *P. calodonta* (SSM 583) appear to be more strongly hooked and pointed than in *P. uniseris* n.sp., otherwise the falcigers of the two species are very similar with a pronounced articulation.

**Habitat.** The species is often found in dead coral substrata amongst encrusting brown algae, coralline and filamentous algae. Some specimens (QM GH 3918), (AM W202847) found amongst pumice washed up on beaches and others have been found to co-occur with *Platynereis polyscalma*.

**Distribution.** Australia (Northern Australia from Rosemary Island, Dampier Archipelago 20°29'S 116°35'E to Herald Group, North East Cay, Queensland 22°07'S 152°17'E).

**Etymology.** The specific name *uniseris* refers to the single row of pectinate bars on the oral ring of the pharynx.

### *Solomononereis* Gibbs

*Solomononereis* Gibbs, 1971: 151.

**Type species.** *Solomononereis marauensis* Gibbs, 1971, by original designation.

**Diagnosis.** Prostomium with 2 antennae, 1 pair of biarticulate palps and 1 pair of eyes. Four pairs of tentacular cirri, dorsal pairs of tentacular cirri long, ventral pairs much shorter. Pharynx with small rod-like paragnaths arranged in 8 discrete groups on maxillary ring; oral ring without paragnaths. Parapodia biramous with spinigers throughout. Notopodial and neuropodial falcigers in median and posterior setigers.

**Remarks.** This genus is monospecific and was originally described from the Solomon Islands, South Pacific by Gibbs (1971) and this is the first record of the genus from outside the type locality.

### *Solomononereis marauensis* Gibbs

*Solomononereis marauensis* Gibbs, 1971: 151-153, fig.8A-H.

**Material examined.** HOLOTYPE: Solomon Islands: Fintry Point, Nggela Island, 9°05'S 160°15'E (BMNH ZB 1970.32). PARATYPES: Solomon Islands: Sandfly Passage, (Florida Islands) 9°00'S 160°06'E 3(BMNH ZB 1970.33).

**Non type material.** Northern Territory: Rose River, Numbulwar tidal flats, 14°20'S 135°41'E, 7 June 1983, 1(NTM W1104); McArthur River, Curie Channel, 15°50'S 136°41'E, intertidal, 7 Aug. 1985 (NTM W3099), (NTM W3106), (NTM W3109), (NTM W3175), (NTM W3176), (NTM W3499), (NTM W3501), (NTM 3748); Gove Peninsula, Drimmie Arm, Mangrove Creek, 12°14'S 136°42'E, 1 June 1973, 1(NTM W537), 9 Jan. 1973, 1(NTM W618), 30 Oct. 1972, 1(NTM W621), 22 Mar. 1972, 1(NTM W622), 3 Nov. 1971, 1(NTM W623), 12 July 1972, several (NTM W625), 30 Oct. 1972, 1(NTM W1373). All specimens collected intertidally.

**Description.** All specimens incomplete, range in size up to 52 mm long, 3.0 mm wide, 118 setigers, 0.5-2.5 mm jaw length. Alcohol preserved specimens pale brown to cream with prominent brownish gland visible below

dorsal cirrus. Prostomium rectangular with antennae arising from extreme corners of distal margin. Palps globular with stout bi-articulate palpophores and small palpostyles. Peristomium relatively narrow. Longest tentacular cirri extends to setiger 20, shortest to setiger 3. Jaws with 8 teeth. Pharynx with paragnaths on maxillary ring arranged as follows: Area I = 1-7, II = 5-12, III = 2-10 medially and 0-7 paragnaths laterally, IV = 3-14; oral ring bare.

Anterior notopodia with elongate, narrow, dorsal cirrus which exceeds length of dorsal ligule. Dorsal and median ligules conical. Neuropodia with conical acicular lobe slightly longer, conical postsetal lobe. Ventral cirrus one half as long as ventral ligule. Posteriorly, dorsal ligule and ventral ligule greatly reduced. In far posterior setigers, dorsal ligule absent and ventral ligule persists as rudiment. Dorsal cirrus increases greatly in length in median and posterior parapodia; in parapodia 50, dorsal cirrus approximately two and a half times as long as dorsal ligule. Notopodia with homogomph spinigers throughout and homogomph falcigers in far posterior setigers. Neuropodia with homogomph and sesquigomph spinigers, and single heterogomph falciger in supra-acicular fascicle; heterogomph spinigers in subacicular fascicle. Falcigers with elongate blade with curved tip and distinct tendon.

**Remarks.** In the original description of *Solomononereis marauensis*, Gibbs records the number of paragnaths in each discrete group on the proboscis as 10-15 and the holotype has the following arrangement of paragnaths:- I = 2-3, II = bundle of 3-4, III = bundle of 7, IV = 5 bundles evenly spaced with each bundle consisting of several pegs closely adjacent to each other, bundle 1 = 5-6, 2=8, 3=8, 4=10, 5=7, bundles 1 and 5 consisting of larger peg-like paragnaths than in other bundles, bundle 3 is the mid central bundle, oral ring bare. The Australian material has the number of paragnaths increasing with the size of the specimen; however, our largest specimens, although similar in size to those examined by Gibbs, tend to have fewer paragnaths in Area IV. In our material the number of paragnaths on each Area varies as follows (greatest to least number of paragnaths): III>IV>II>I. Other characters, however, particularly of the parapodia and setae, agree well with the type material. This extends the distribution of this monospecific genus considerably, from the Solomon Islands, South Pacific to northern Australia.

**Habitat.** In Australia this species has been found in mangrove-lined creeks subjected to wide fluctuations in salinity. Specimens from the Solomon Islands were found in sticky mud above midtide level close to freshwater outflows.

**Distribution.** Australia (northern Australia from 14°20'S 135°41'E to 12°14', 136°42'E), Solomon Island (type locality).

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# A Revision of the Australian Species of *Iphiaulax* Foerster and *Chaoilta* Cameron (Insecta: Hymenoptera: Braconidae)

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ABSTRACT. Identification keys are provided for the Australian species of *Iphiaulax* Foerster and *Chaoilta* Cameron. *Iphiaulax brunneipennis* n.sp. from Victoria, *Iphiaulax latistigma* n.sp. from Queensland and the Solomons, *Iphiaulax danielsi* n.sp. from New South Wales, and *Chaoilta hollowayi* n.sp. from New South Wales, Queensland and Western Australia are described and illustrated. *Iphiaulax australiensis* Ashmead, *I. dubitorius* (Fabricius), *I. innotatus* (Turner), *I. proficiscator* (Fabricius), *I. rufus* Szépligeti, *C. decorata* (Szépligeti), *C. insularis* (Cameron), *C. lutea* Cameron and *C. nigriceps* (Cameron) are redescribed and illustrated. *Blastomorpha* Szépligeti, previously synonymised with *Chaoilta*, is raised in status to that of a subgenus of *Chaoilta*. *Ichneumon hospitator* Fabricius is treated as a junior synonym of *Iphiaulax proficiscator* (Fabricius) and *Iphiaulax turneri* Baltazar is treated as a junior synonym of *Ichneumon dubitorius* Fabricius. Two species are removed from *Iphiaulax* : *rubricepsis* Shenefelt to the Doryctinae and *trinotata* Ashmead to *Bracon* Fabricius. Distribution maps and flight period histograms are provided for the four commonest species of *Iphiaulax* viz. *I. australiensis*, *I. dubitorius*, *I. proficiscator* and *I. rufus*. Two species of *Chaoilta* are recorded from Australia for the first time, viz. *C. insularis* and *C. lutea*.

QUICKE, D.L.J., 1991. A revision of the Australian species of *Iphiaulax* Foerster and *Chaoilta* Cameron (Insecta: Hymenoptera: Braconidae). Records of the Australian Museum 43(1): 63–84.

The Australian species of two genera of parasitic, braconine wasps are revised. These genera, *Iphiaulax* Foerster and *Chaoilta* Cameron, comprise a number of moderately sized to large, and often brightly coloured insects and include several common Australian species, though these have been little-studied in the past.

Few braconine genera have been so frequently misinterpreted as has *Iphiaulax*. Species of *Iphiaulax* are frequently common, large and brightly coloured, and consequently, they are often collected and many of them have been described; approximately 520 species are listed in Shenefelt (1978). Several species were common and conspicuous enough to have been included in early systematic collections from Australia and thus three species names date back to the late eighteenth century works of Fabricius (see also Zimsen, 1964).

Despite the fact that *Iphiaulax* is an easily characterised genus (Quicke, 1986, 1987, 1988a), the Australian species have often been placed under other generic names, the most common of these being *Cyanopterus* Haliday and *Bracon* Fabricius, both of which are valid and distinct genera. Particular authors were inconsistent in their placements of *Iphiaulax* species as several placed great emphasis on whether or not the second metasomal suture was crenulate. Thus *Iphiaulax* species with a crenulate suture were usually identified correctly as *Iphiaulax* but those with a smooth suture were often placed in *Cyanopterus* which they superficially resemble. Thus the Australian species of *Cyanopterus* treated in Turner's (1918) key are in fact species of *Iphiaulax*, while in the same paper he described another species of *Iphiaulax* under the correct generic name. The same artificial splitting of *Iphiaulax* was also made by Szépligeti (1904, 1906). To confuse matters even further, species belonging to other genera have often been misidentified as belonging to *Iphiaulax*, and in Australia this has been particularly true for species of the common genus *Poecilobracon* Cameron. Given this confusion, the Australian species have been revised, each is described and illustrated. A key to species, distribution maps and flight period histograms for the commoner species are provided.

Members of the genus *Chaoilta* Cameron are usually medium-sized to large braconine wasps, and are found from India through to Australia and on some of the larger islands of Oceania. *Chaoilta* belongs to the cosmopolitan *Atanycolus* Foerster group of genera (Quicke, 1987) as is evidenced by the complex form of the scapus and pedicellus (Fig.7a). In addition, *Chaoilta* species are typically more or less strongly dorsoventrally compressed, and possess characteristic facial architecture with a transverse, sharply projecting ledge shortly below the antennal sockets (Fig.7a-c). These features collectively make *Chaoilta* one of the world's more distinctive of braconine genera, and consequently relatively easy to identify.

Only two species of *Chaoilta* have been recorded from Australia (Parrott, 1953) although rather more have been described from Papua New Guinea, Indonesia and the Philippines, bringing the total number of species described from that part of the world to 33 (Shenefelt, 1978; see both *Chaoilta* and *Platybracon*). However, several of these may prove to be synonyms when the species of the whole region are revised. A total of five Australian species were found as a result of the present study, one of which is new and is described and illustrated below. An illustrated key to the Australian species of *Chaoilta* is provided.

Terminology follows that of van Achterberg (1979, 1988) with additions and modifications according to Quicke (1989). Thus, ovipositor length, unless stated otherwise, is taken as the length of that part which extends beyond the apex of the metasoma when the ovipositor is directed posteriorly, and the width of the first metasomal tergite refers to the maximum width of the sclerotised tergum.

The following definitions, ratios and abbreviations are used: tentorial ratio = height of clypeus : inter-tentorial distance : tentorio-ocular distance; facial ratio = width of face : width of head : height of eye; ocellar ratio = postocellar length : transverse diameter of posterior ocellus : shortest distance between posterior ocellus and eye; head index = length of head behind eye/ horizontal length of eye; radial sector ratio = length of vein SR1 : length of 3-SR : length of r; submarginal cell ratio = length of vein 2-SR; length of 3-SR : length of r-m; pterostigmal index = length of pterostigma/ maximum width of pterostigma; hindwing vein ratio = length of vein 1r-m : length of vein SC+R1; fore leg ratio = length of fore femur excluding trochantellus : length of fore tibia : length of fore tarsus; fore basitarsal index = length of fore basitarsus/maximum depth of fore basitarsus; hind leg ratio = length of hind femur excluding trochantellus : length of hind tibia : length of hind basitarsus; hind basitarsal index = length of hind basitarsus/maximum depth of hind basitarsus.

Note that some of these characters are only used in connection with descriptions of species in one of the two genera treated here. For example, the tentorial ratio cannot be applied easily to members of the genus *Chaoilta* because of their modified, compressed faces, while the head index is of no practical value in dealing with *Iphiaulax* species as head shape is relatively uniform across the genus. Figures are shaded as if illuminated from the upper right. Specimen data are arranged by state and are given as : number of each sex, locality, notes (if any) collection date (month and year), and collection (in parentheses).

Collections containing material relevant to this study are abbreviated as follows: Australian Museum, Sydney (AM); Australian National Insect Collection, Canberra (ANIC); Bishop Museum, Honolulu (BMH); British Museum (Natural History), London (BMNH); Department of Primary Industries, Entomology Branch, Brisbane (DPIB); Hungarian Natural History Museum, Budapest (HNHM); Queensland Museum, Brisbane (QM); Queensland University, St Lucia (QU); Quicke Collection (QC); United States National Museum, Washington DC (USNM); Western Australian Museum, Perth (WAM).

## Systematics

### *Iphiaulax* Foerster, 1862

*Iphiaulax* Foerster, 1862: 235.–Parrott, 1953: 207.
*Aniphiaulax* Kokoujev, 1899: 408 (*Vipio* (*Aniphiaulax*) *jakowlewi* Kokoujev, 1899, monotypy).
*Iphiaulacidea* Fahringer, 1926: 203 (*Ichneumon impostor* Scopoli, 1763, designated by Muesebeck & Walkley, 1951).
*Euglyptobracon* Telenga, 1936: 104 (*Bracon umbraculator* Nees von Esenbeck, 1834, original designation).

**Type species.** *Ichneumon impostor* Scopoli, 1763, monotypy.

**Description.** *Female.* Antennae longer than forewing, tapering gradually from base to apex. Median flagellomeres much wider than long. Scapus large, longer ventrally than dorsally in lateral aspect, apicolaterally strongly emarginate, distinctly apicomedially emarginate. Lower part of clypeus strongly reflexed into the hypoclypeal depression. Eyes almost glabrous. Frons not or hardly impressed behind the antennal sockets, with a midlongitudinal sulcus, glabrous. Head narrowing behind the eyes. Mesosoma smooth and shiny. Mesoscutum largely glabrous, notauli weak. Scutellar sulcus narrow and usually crenulate. Precoxal suture absent. Mesopleural suture smooth. Propodeum without carinae or coarse sculpture Forewing vein 3-SR more than 1.9 times length r-m (usually more than 2.2 times). Forewing vein r-m with 2 bullae. Vein SR1 reaching wing margin more than 0.9 of the distance between the pterostigma and the wingtip. Vein 1-SR+M more or less straight. Veins 1-SR and C+SC+R forming an angle of 50-60°. Vein cu-a interstitial or slightly postfurcal. Vein 3-CU1 not or only weakly expanded posteriorly. Hindwing vein 1r-m usually slightly shorter than vein SC+R1. Base of hind wing with glabrous area immediately distal to vein cu-a. Apex of hindwing vein C+SC+R with more than 1 especially thickened bristle. Claws simple with rounded basal lobe. First metasomal tergite with complete, sublamelliform dorsolateral carinae, without dorsal carinae; raised median area smooth or sculptured, rarely (*I. australiensis*, see below) with a midlongitudinal carina. Second metasomal tergite considerably wider than long, without a distinct midbasal raised triangular area, with pair of sublateral grooves which curve towards one another anteriorly. Second suture smooth or crenulate. Third tergite with distinct posteriorly-diverging, anterolateral grooves. Tergites 3-5 with transverse, subposterior grooves; posterior margins fully sclerotised and distinctly curved in profile. Ovipositor robust, usually 0.5-1.0 times length of metasoma; without preapical dorsal nodus and without distinct preapical ventral serrations.

*Male.* Generally similar to females but often smaller. Mesosoma relatively more elongate in males. Genitalia with an extremely elongate, often medially with a strongly produced basal ring (Fig.4); parameres and volsellae with few setae; digitus with single apical tooth (Quicke, 1988d). Rectum not fused to eighth abdominal tergite and intertergal gland between seventh and eighth abdominal terga small (Quicke, in press).

**Biology.** *Iphiaulax* is a widespread genus within the Old World with many described species, though records from the New World all appear to be referable to the superficially similar genus, *Digonogastra* Viereck (Quicke, 1988a). *Iphiaulax* species are idiobiont ectoparasitoids and the majority of reliable host records indicate the members of this genus primarily attack cerambycid beetle larvae (Quicke, 1988b), though some species do appear to parasitise other hosts even including concealed Lepidoptera larvae.

Little is known about the hosts of Australian species of *Iphiaulax*. One specimen of *I. dubitorius* in the DPIB collection is labelled as being bred from a 'citrus stemborer larva', probably the cerambycid, *Platymopsis pulverulens* (Boisduval), and a specimen of *I. proficiscator* in the ANIC is recorded as having emerged from a Mimosa branch that appeared to have been bored-out by cerambycids. These records therefore support the contention that Australian *Iphiaulax* species are also principally parasites of Cerambycidae. The few published records of *Iphiaulax* which indicate other hosts should therefore be treated with caution, particularly as members of other genera of wasps were frequently misidentified as belonging to *Iphiaulax* in the past. Nevertheless, three papers reporting host records for Australian *Iphiaulax* should be noted. Newman & Clark (1924) reported on *Iphiaulax* species as having been reared from the tuart bud weevil, *Cryptoplus* [as *Haplonyx*] *tibialis* (Lea). However, examination of their photograph suggests that the braconid concerned belongs to some other genus (possibly *Poecilobracon*) as the female has a relatively longer ovipositor than most Australian *Iphiaulax* and the wing pattern does not agree well with that of any of the known Australian species. Chadwick & Nikitin (1976) also record an unidentified *Iphiaulax* sp. from a weevil host, *Oemethylus triangularis* Lea. Unfortunately the author has not been able to examine their specimen but as they note the species as belonging to *Iphiaulax sensu lato* it may well belong to some other genus. Chadwick & Nikitin (loc. cit.) also provide a host record for *I. rubriceps* Froggatt, but this species belongs to the Doryctinae (see below). Finally, Champ (1966) reports an *Iphiaulax* as a parasite of the gelechiid pest, *Scrobipalpa heliopa* (Lower). Again the author has not been able to examine the material, however, the record seems unlikely on the basis of the other known hosts.

## Key to the Australian Species of *Iphiaulax*

(females only)

1. Pterostigma more than 2.4 times longer than wide (Fig.1b-f); pterostigma largely yellow; metasoma largely yellow to red (at least tergites 1-3) ..... 2

—— Pterostigma less than 2.3 times longer than wide (Fig.1a); pterostigma ivory-white; metasoma largely black or piceous ..... *I. latistigma* n.sp.

2. Metasoma with a piceous-brown or black apex (at least tergites 5-7); hind femur largely black ..... 3

—— Metasoma entirely yellow, orange or red; hind femur entirely orange or yellow ..... 6

3. Mesosoma with at least the mesoscutum and propodeum black; second metasomal suture crenulate (Fig. 2b,d); total ovipositor length less than 0.75 times forewing length ..... 5

—— Mesosoma without black markings; second metasomal suture completely smooth (see Fig.2c); total ovipositor length more than 0.75 times forewing length ..... 4

4. Fore and mid legs entirely black; forewing including pterostigma entirely brown (Fig.3b); fourth metasomal tergite black ..... *I. brunneipennis* n.sp.

—— Fore and mid legs orange-yellow except for tarsi; forewing with basal 0.4 yellow and pterostigma with basal 0.7 yellow; fourth metasomal tergite orange-yellow ..... *I. danielsi* n.sp.

5. First metasomal tergite with a well-developed midlongitudinal carina (Fig.2a); scutellum piceous brown or black; ovipositor preapically approximately 1.4 times deeper than the diameter of the second flagellomere (Fig.2e); hind trochanters piceous brown or black ..... *I. australiensis*

—— First metasomal tergite without a midlongitudinal carina or ridge; scutellum yellow or orange-red; ovipositor pre-apically less deep than diameter of the second flagellomere (Fig.2f); hind trochanters yellow ..... *I. dubitorius*

6. Forewing boldly patterned brown on yellow (Fig.1c-f) ..... 7

—— Forewing almost entirely brown, only the pterostigma, a small area below this and the extreme base yellowish (Fig.1b) ..... *I. innotatus*

7. Forewing with a broad yellow band extending transversely from below pterostigma to, or nearly to, the posterior wing margin (Fig.1e) ..... *I. proficiscator*

—— Forewing with a smaller clear area in the first submarginal cell extending just into the second subdiscal cell (Fig.1d) ..... *I. rufus*

### *Iphiaulax australiensis* Ashmead

Figs 1c, 2a,b,e, 4a, 5a, 6a

*Iphiaulax australiensis* Ashmead, 1900: 360 (not Szépligeti 1905, 1906).–Szépligeti, 1904: 23.
*Hybogaster australiensis*.–Roman, 1915: 15.–Parrott, 1953: 207.–Shenefelt, 1978: 1689.

**Material examined.** HOLOTYPE male labelled "Australia" (USNM).

New South Wales: 1 male, 1 female, Round Hill Fauna Reserve, Oct. 1977 (AM); 1 female, Lane Cove Sydney, Oct. 1946 (AM); 1 male, Sydney, no date (AM); 1 female, Cobar, Oct. 1957 (ANIC). Northern Territory: 1 female, Alice Springs, Feb. 1966 (ANIC); 1 female, Alice Springs, Sept. 1978 (QC). Queensland: 1 male, Boulia, Oct. 1978

(ANIC); 2 females, Julian Creek, July 1932 (DPIB); 1 female, Kiata, Dec. 1918 (AM); 1 female, Kihee, Oct. 1949 (ANIC); 1 female, Quondong, 7 mi (= 11 km) west of Tarco, no date (ANIC). South Australia: 1 female, Mount Illibillee, Everard Ranges, May 1988 (AM); 1 female, Elizabeth Springs, May 1981 (AM); 1 female, Quorn, Apr. 1978 (ANIC); 1 male, Lyndhurst, Sept. 1972 (ANIC); 1 male, Brachina, Nov. 1987 (ANIC); 1 female, Broken Hill, Nov. 1949 (ANIC). Western Australia: 1 male, Yalgoo, Sept. 1981 (AM); 1 female, Duri, Feb. 74 (AM); 1 female, Fremantle, Apr. 1934 (ANIC); 1 male, Kalbarri, Nov. 1971 (ANIC); 1 female, Hopetown, Jan. 1987 (QU); 1 male, Murchison River near north-west Coastal Highway crossing, Jan. 1976, "on *Eucalyptus* sp." (QU); 1 male, Lake Grace, no date (WAM); 2 females, Forrest Dale, no date (WAM); 1 female, Tallering Stn, Sept. 1976 (WAM); 1 female, 37 km south-west of Glenayle HS, Aug. 1983 (WAM); 1 male, King's Park, Mar. 1964 (WAM); 1 female, 9.75 km north-north-west of Mount Linden, Mar. 1979, "feeding on lerps on *Eucalyptus*" (WAM); 1 female, Millstream, July 1958, "on flowers of *Acacia*" (WAM); 1 female, 8.4 km north-north-west of Cataby, Jan. 1983 (WAM); 1 male, Cadoux, Oct. 1981 (WAM); 1 female, 7 km north-west of Hamersby Inlet, Nov. 1979, "flying near dead branch of *Eucalyptus tetragena*" (WAM); 1 male, Reserve 6 km east-north-east of Meredin, Oct. 1978 (WAM).

**Description.** *Female.* Length of body 10-13 mm, length of forewing 10-13 mm and length of ovipositor (part exserted beyond the apex of the metasoma) 3-5 mm. Antenna with approximately 100 flagellomeres. Tentorial ratio = 1.23:1.0. Face densely with long (yellow) setae, with deep punctures at bases of setae, smooth and shiny between punctures. Facial ratio = 1.0: 1.94:1.0. Frons broadly depressed, with well-developed midlongitudinal sulcus, smooth, shiny and glabrous except for row of setae near margin of eye. Ocellar ratio = 1.36:1.0 2.24. Mesosoma 1.65 times longer than high. Scutellar sulcus totally smooth. Propodeum moderately longsetose laterally, more sparsely so medially. Radial sector ratio = 5.76: 3.46:1.0. Submarginal cell ratio = 1.25:2.25:1.0. Pterostigmal index = 2.8. Vein 1-SR+M very weakly sinuate. Vein cu-a more or less interstitial. Vein 3-CU1 distinctly swollen posteriorly. Hindwing vein ratio = 1.0:1.06. Apex of hindwing vein C+SC+R with 3-6 especially thickened bristles. Fore leg ratio = 1.0:1.23:1.7. Hind leg ratio = 1.95:3.0:1.0. Hind basitarsal index = 5.4. First metasomal tergite approximately 1.3 times wider than long; with well-developed dorsolateral carinae which run more or less in parallel to the posterior margin of the tergite where they are moderately widely removed from the edge of the tergite; raised median area with a well-developed midlongitudinal carina, with irregular deep foveate sculpture especially posteriorly, bordered by a few short crenulae especially anteriorly. Second

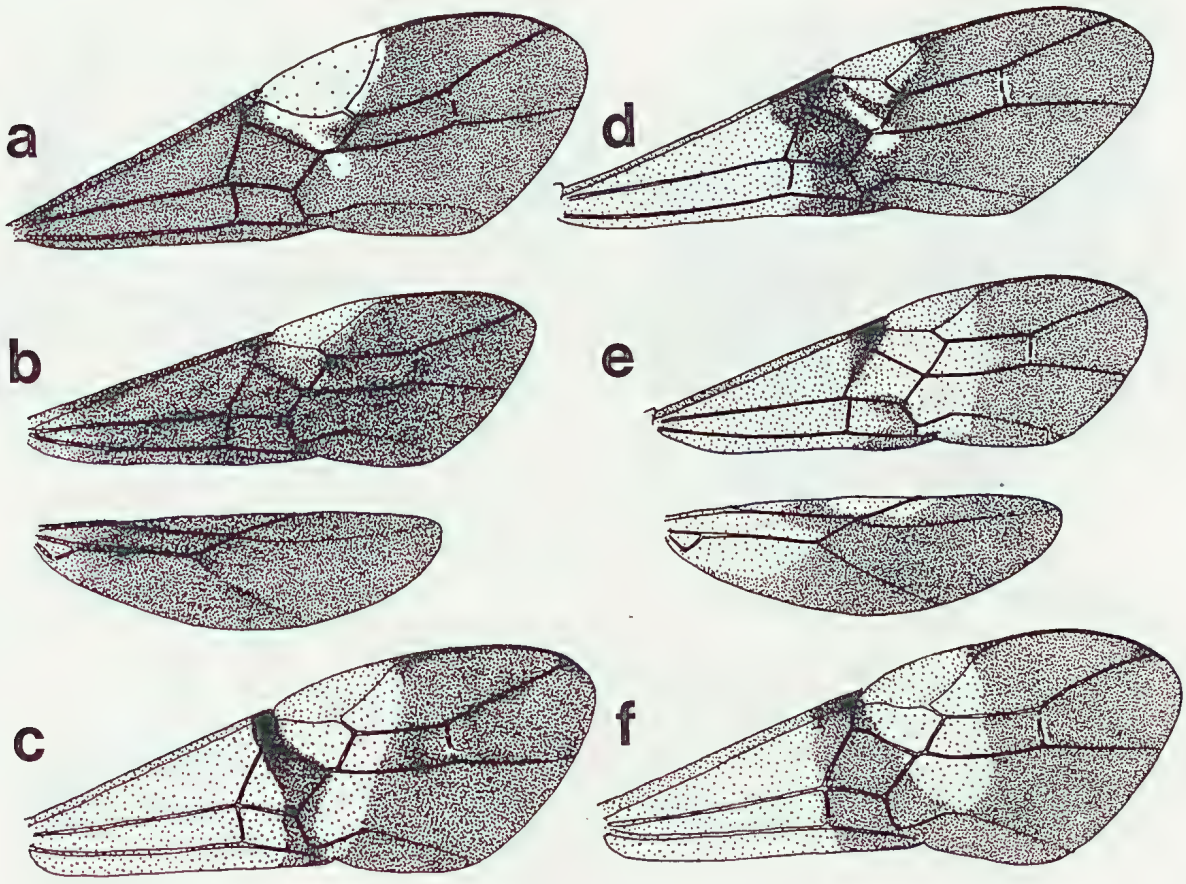


**Fig.1.** Wing colour patterns – a, *I. latistigma* n.sp.; b, *I. innotatus* c, *I. australiensis*; d, *I. rufus*; e, *I. proficiscator*; f, *I. dubitorius*. Scale bar: a–e, 0.25 mm; f, 0.2 mm.

metasomal tergite between the (crenulate) sublateral grooves with foveate rugose sculpture. Second tergite 2.0 times wider than medially long. Second suture wide, deep and finely crenulate. Third tergite with a well-developed subposterior, crenulate groove; smooth apart from the crenulate grooves. Fourth to sixth tergites smooth and each with a smooth subposterior groove. Ovipositor very robust, deepening from near the base to the preapical region; maximum depth more than 1.3 times the diameter of the basal flagellomere. Yellow to yellow-orange except for the following which are black: antennae, a stripe from eye to eye across the top of the head, mesoscutum, scutellum, mesopleuron, mesosternum, metanotum, metapleuron, propodeum, mid-coxa, mid-trochanter, mid-femur (except the apical quarter), hind coxa, trochanter, femur, tibia (except for the basal quarter), tarsus, metasomal tergites 5-7, ovipositor sheaths. Wings yellow with a narrow transverse dark brown band below the parastigma of the forewing, and an extensive mid-brown apical zone on both the fore and hind wings.

*Male*. As for females though generally somewhat smaller. Genitalia with extensively and densely setose parameres. Volsellae broadly, densely setose. Digitus with

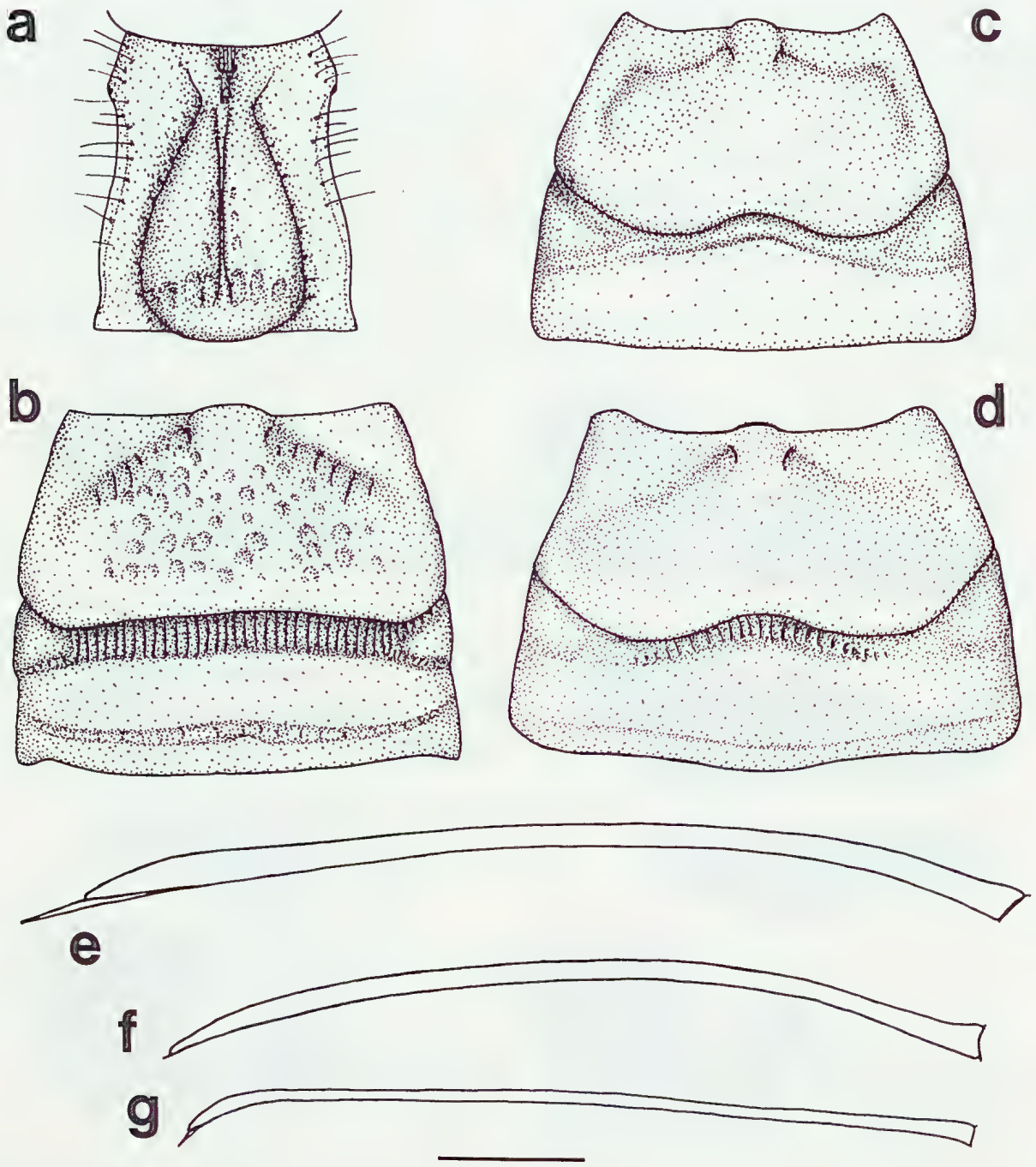


**Fig.2.** Metasomal and ovipositor features – a,b, *I. australiensis*; c, *I. rufus*; d, *I. dubitorius*; e, *I. australiensis*; f, *I. dubitorius*; g, *I. danielsi* n.sp. Scale bar: a–c, 1.0 mm; d, 1.5 mm; e,f, 0.8 mm; g, 1.8 mm.

one apical tooth-like process. Basal ring very elongate.

**Notes.** Collection dates indicate that adults of this species are probably active throughout the year but are relatively more abundant around October (Fig.5a). *Iphiaulax australiensis* is the most widely distributed of the Australian *Iphiaulax* species (Fig.6a) though there are no records from north of 20° and the author is not aware if any specimens from Victoria, Tasmania, nor of any from outside of Australia. It should be noted that unlike the other Australian species, *I. australiensis* has been collected frequently from the interior and also from the south west.

*Iphiaulax australiensis* is a highly aberrant species differing from more typical *Iphiaulax* not only in the presence of a strong midlongitudinal carina on the first metasomal tergite (Fig.2a) but also in the densely setose parameres of the male genitalia (Fig.4a). These differences are sufficient to warrant asking whether or not *australiensis* should be placed in *Iphiaulax* or in a new genus. In particular, extensively setose parameres are usually considered to be plesiomorphic whereas largely glabrous (except for the apical margin) ones as found in other *Iphiaulax* (Fig.4b) are considered apomorphous (Quicke, 1988d). Thus, *australiensis* can only readily be included in *Iphiaulax* if its setose parameres are considered an independent apomorphous feature. Significantly, *Iphiaulax* species, together with those of some possibly related genera (eg. *Plaxopsis* Szépligeti, *Pseudovipio* Szépligeti & *Zanzopsis* van Achterberg), have the basal ring particularly strongly produced anteroventrally (Quicke, 1988a,d). In *I. australiensis* the basal ring is very strongly produced anteriorly and therefore it seems reasonable to assume, at least for the present, that the setose parameres and carinate first tergite are indeed peculiarities of *I. australiensis* and that it should be retained within *Iphiaulax*.

### *Iphiaulax brunneipennis* n.sp.

Fig.3a–d

**Material examined.** HOLOTYPE female labelled "c.

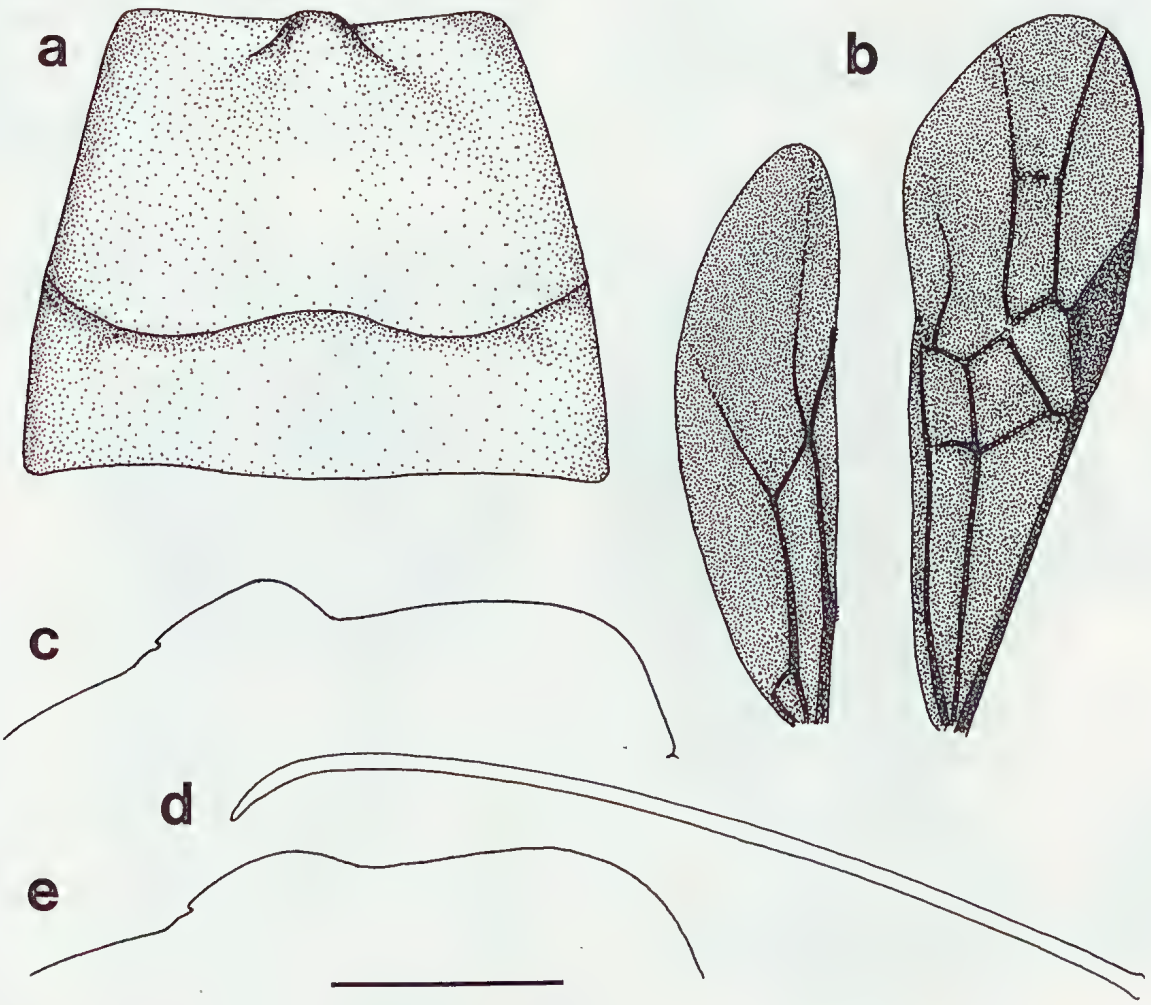


**Fig.3.** a–d, *I. brunneipennis* n.sp. – a,d: a, metasomal tergites 2+3; b, wings; c, dorsal profile of mesosoma; d, ovipositor. e; *I. danielsi* n.sp. – dorsal profile of mesosoma. Scale bar: a, 1.0 mm; b, 3.0 mm; c,e, 1.2 mm; d, 2mm.

7.2.01 Victoria" and "R.E. Turner. 1909-123" (NHM).

**Description.** *Female*. Length of body 8.8 mm, of forewing 9.0 mm and of ovipositor (part exserted beyond apex of metasoma) 6.6 mm. First flagellomere 1.0 and 1.2 times longer than the second and third respectively, the latter 1.07 times longer than deep. Tentorial ratio = 1.0:2.5:2.0. Face with only small punctures at bases of setae, smooth and shiny between these. Facial ratio = 1.0:1.76:1.05. Frons with a few setae on lateral 0.25, otherwise glabrous and shiny. Ocellar ratio = 1.0:1.0:2.17. Mesosoma 1.64 times longer than high. Scutellar sulcus distinctly though rather weakly crenulate. Scutellum strongly protruding in lateral aspect. Propodeum moderately densely long setose laterally, sparsely setose medially. Radial sector ratio = 7.5:5.5:1.0. Submarginal cell ratio = 1.0:2.5:1.0. Pterostigmal index = 2.8. Vein 1-SR+M nearly straight. Vein cu-a marginally postfurcal. Vein 3-CU1 not expanded posteriorly. Hindwing vein ratio = 1.0:1.18. Apex of hindwing vein C+SC+R with 4 especially thickened setae. Fore leg ratio = 1.0:1.1:1.62. Hind leg ratio = 1.79:2.65:1.0. Hind basitarsal index = 6.0. First metasomal tergite 1.35 times longer than wide. Second tergite 1.9 times wider than medially long. Second suture sinuate and smooth. Third metasomal tergite with poorly defined anterolateral areas. Fourth and fifth tergites with smooth, transverse, subposterior grooves. Ovipositor approximately 3.45 times longer than medial length of syntergite 2+3; total length approximately 1.18 times longer than forewing; apically strongly down-curved; maximum depth (preapical) equal to diameter of third flagellomere. Red-orange except for the following which are black (or piceous): antennae, head, legs, metasomal tergites 4-8, ovipositor sheaths. Wings uniformly brown with dark brown pterostigma and venation.

**Etymology.** Name refers to uniformly brown wings.

### *Iphiaulax danielsi* n.sp.

Figs 2g, 3e

**Material examined.** HOLOTYPE female, labelled "47 km NE Inverell NSW 8 Jan 1978 G. Daniels." (QU).

**Description.** *Female*. Length of body 9 mm, of forewing 10 mm, and of ovipositor (part exserted beyond apex of metasoma) 7.7 mm. Antenna with 94 flagellomeres. Terminal flagellomere acuminate. Tentorial ratio = 1.0 : 2.45 : 1.96. Face shiny between puncture, at the bases of (black) setae. Facial ratio = 1.0:2.1:1.06. Frons glabrous, weakly, broadly impressed with midlongitudinal sulcus. Ocellar ratio = 1.0:1.1:2.4. Mesosoma 1.7 times longer than high. Scutellar sulcus

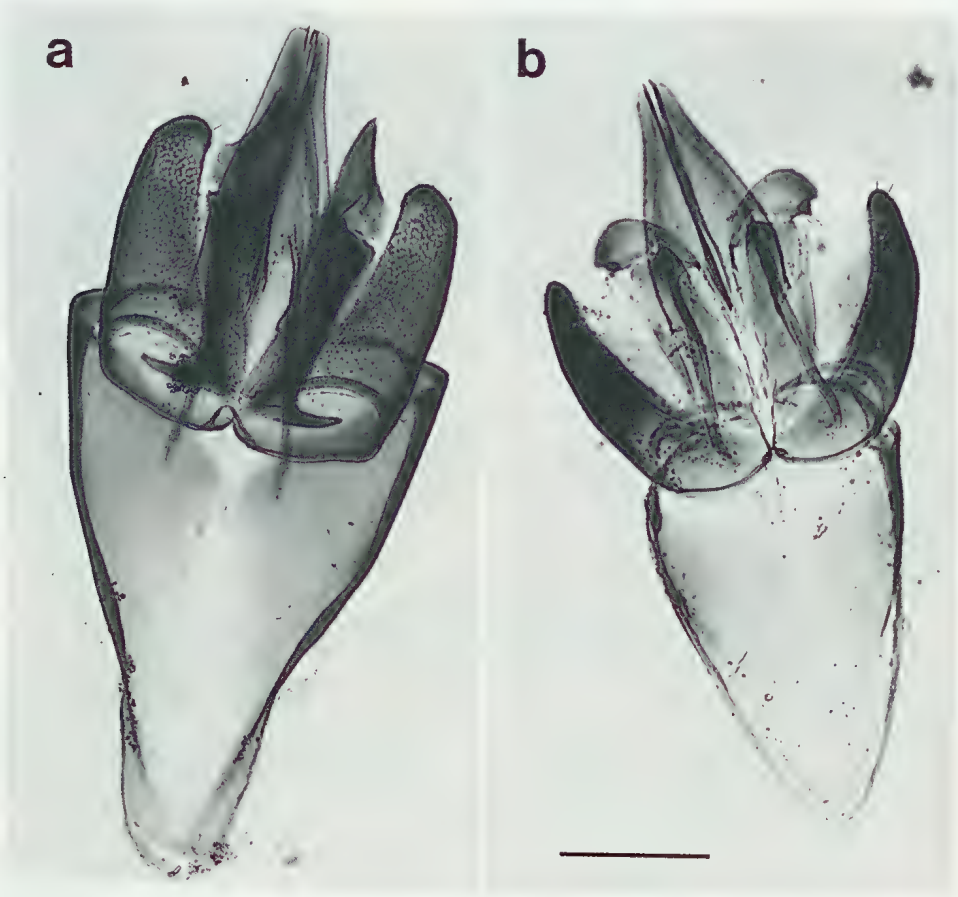


**Fig.4.** Male genitalia – a, *I. australiensis*; b, *I. dubitorius*. Scale bar: a,b, 0.25 mm.

totally smooth. Propodeum densely long-setose laterally, sparsely setose medially. Radial sector ratio = 5.28:4.0:1.0. Submarginal cell ratio = 1.0:2.38:1.0. Pterostigmal index = 2.8. Vein 1-SR+M more or less straight. Vein cu-a marginally postfurcal. Vein 3-CU1 not expanded posteriorly. Hindwing vein ratio = 1.0:1.22. Apex of hindwing vein C+SC+R with 6 thickened setae. Fore leg ratio = 1.0:1.12:1.4. Hind leg ratio = 1.83:2.59:1.0. Hind basitarsal index = 5.75. First metasomal tergite 1.53 times longer than maximally wide. Second tergite 2.04 times wider than medially long. Second suture sinuate and smooth. Fourth and fifth tergites with smooth, transverse, subposterior grooves. Ovipositor approximately 3.4 times longer than medial length of syntergite 2 + 3; total length approximately equal to forewing length; maximum depth (preapical) 1.03 times diameter of basal flagellomeres. Orange yellow except for the following which are black (or piceous): antennae, head except palps, mid-tarsus, hind coxa (except base and apex), hind trochanter (except dorsally), hind femur (except trochantellus and extreme apex), hind tibia except base, hind tarsus, metasomal tergites 5-8, hypopygium and ovipositor sheaths. Wings with basal 0.4 yellow, remainder dark brown-grey except pterostigma yellow for basal 0.7 and a small posteriorly narrowing clear zone posterior to pterostigma.

**Etymology.** Named in honour of G. Daniels, the collector.

**Notes.** Closely related to *I. brunneipennis* n.sp. differing from it principally in colouration though *I. brunneipennis* has a distinctly crenulate scutellar sulcus and smaller glabrous area at the base of the hind wing.

### *Iphiaulax dubitorius* (Fabricius)

Figs 1f, 2d,f, 4b, 5d, 6b

*Ichneumon dubitorius* Fabricius, 1775: 331.
*Iphiaulax transiens* Turner, 1918: 95 (non Szépligeti, 1904:173) n.syn.–Parrott, 1953: 208.
*Iphiaulax turneri* Baltazar, 1972: 275 [replacement name] n.syn.–Shenefelt, 1978: 1800.

**Material examined.** HOLOTYPE female of *dubitorius* with no data (BMNH; Banks Collection). HOLOTYPE female of *transiens* labelled "*Iphiaulax transiens* Type Turn.", "Type H.T." & "B.M. TYPE HYM. 3.c. 366" (BMNH; 3.c. 366).

New South Wales: 1 female, Trial Bay, Dec. 1929 (AM). Northern Territory: 1 male, "The Esplanade", Darwin, Aug. 1970 (AM); 1 male, Oenpelli, June 1973 (ANIC); 1 female, Mount Cahill, June 1973 (ANIC); 1 female, Mudginbarry, June 1973 (ANIC); 1 female, Barooola, Apr. 1976 (ANIC); 1 male, Rimbija Island, Wessel Islands, Feb. 1972 (ANIC); 1 male, Borradaile, Nov. 1972 (ANIC); 1 female, Darwin, Oct. 1972 (ANIC); 1 female, Holme's Jungle, Berrimah, July 1979 (QM); 1 female, Port Darwin, no date (BMNH). Queensland: 2 females, Ayr, Sept. 1950 (ANIC); 1 female, Biggenden, May 1973 (ANIC); 1 female, Bin Bin Range, Jan. 1975 (ANIC); 1 female, Bluff Range, Apr. 1975 (ANIC); 1 male, Bluff Range, Nov. 1976 (ANIC); 1 male, Bundaberg, Nov. 1971 (ANIC); 1 male, Bundaberg, June 1972 (ANIC); 1 female, Bundaberg, July 1972 (ANIC); 1 male, Forty Mile Scrub National Park, July 1986 (ANIC); 1 male, Heron Island, May 1978 (ANIC); 1 female, Laura, June 1975 (ANIC); 1 female, Laura, June 1976 (ANIC); 1 male, Burleigh, Sept. 1940 (DPIB); 1 male, Mackay, Apr. 1879 (ANIC); 1 male, Mackay, July 1918 (ANIC); 1 female, Mossman, July 1971 (ANIC); 5 males, 1 female, Sue (Warraber) Island, Dec. 1977 (ANIC); 1 female, Sue Island, May 1985 (QC); 1 male, Ingham, Mar. 1961 (ANIC); 1 male, Thursday Island, "open forest", Nov. 1976 (ANIC); 1 male, Charters Towers, "on rough lemon", June 1959 (ANIC); 1 male, Cordeles, May 1958 (ANIC); 1 female, Electra, Nov. 1976 (ANIC); 1 female, Koah, "citrus orchard", Mar. 1976 (DP1B); 1 female, Halifax, May 1919 (BMH); 6 females, Halifax, June 1919 (BMH); 1 female, Halifax, July 1919 (BMH); 12 females, 5 males, Mackay, 1909 (BMNH); 6

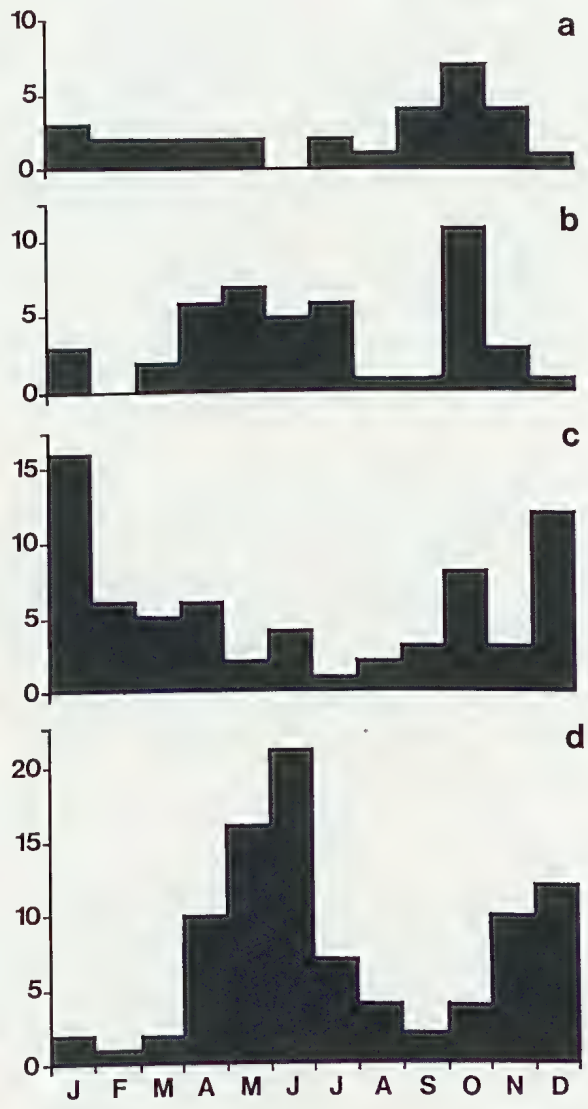


**Fig.5.** Collection date histograms – a, *I. australiensis*; b, *I. proficiscator*; c, *I. rufus*; d, *I. dubitorius*. Note: specimens with collection dates spanning more than one calendar month not included.

females, 1 male, Kuranda, May–June 1913 (BMNH); 1 male, Kuranda, June 4 (BMNH); 2 females, Desailly Creek, 10 km west by north of Mount Carbine, May 1981 (QC); 1 female, Yeppoon, Dec. 1969 (QC); 1 male, Mount Webb, Oct. 1980 (QC); 1 female, Mount Webb National Park, Apr. 1981 (QC); 1 female, Atherton,Dec. 1959 (QC); 1 female, Mount Cook National Park, Oct. 1980 (QC); 1 male, Dunk Island, Sept. 1927 (QM); 1 male, Dent Island, July 1980 (QU); 1 male, Dent Island, Aug. 1980 (QU); 1 female, Saint Lucia, Apr. 1957 (QU); 1 female, Millaroo, Nov. 1965 (QU); 2 males, Yeppoon, Dec. 1979. Western Australia: 1 female, Cape Bertholet, Apr. 1977 (ANIC); 1 male, Drysdale River, Aug. 1975 (ANIC); 1 female, Mitchell Plateau, May 1983 (ANIC); 1 male, 1 female, Marun, June 1988 (ANIC); 1 female, Morgan Falls, Aug. 1975 (ANIC).

**Description.** *Female*. Length of body 5.0-10.0 mm, of forewing 5.5-11.0 mm and ovipositor (part exserted beyond the apex of the metasoma) 1.8-2.6 mm. Antennae with approximately 83 flagellomeres. Tentorial ratio = 1.0:3.5:1.25. Face moderately densely long setose, with deep punctures at bases of setae. Facial ratio = 1.0:1.82. Frons glabrous, broadly, shallowly impressed with deep midlongitudinal sulcus. Ocellar ratio = 1.18:1.0:1.82. Mesosoma 1.75 times longer than high. Notauli very weakly impressed, indicated by few setae. Scutellar sulcus narrow with few weak transverse carinae. Propodeum moderately densely long setose laterally, sparsely setose medially. Radial sector ratio = 4.15:3.0:1.0. Submarginal cell ratio = 1.0:2.0:1.0. Pterostigmal index = 2.6.

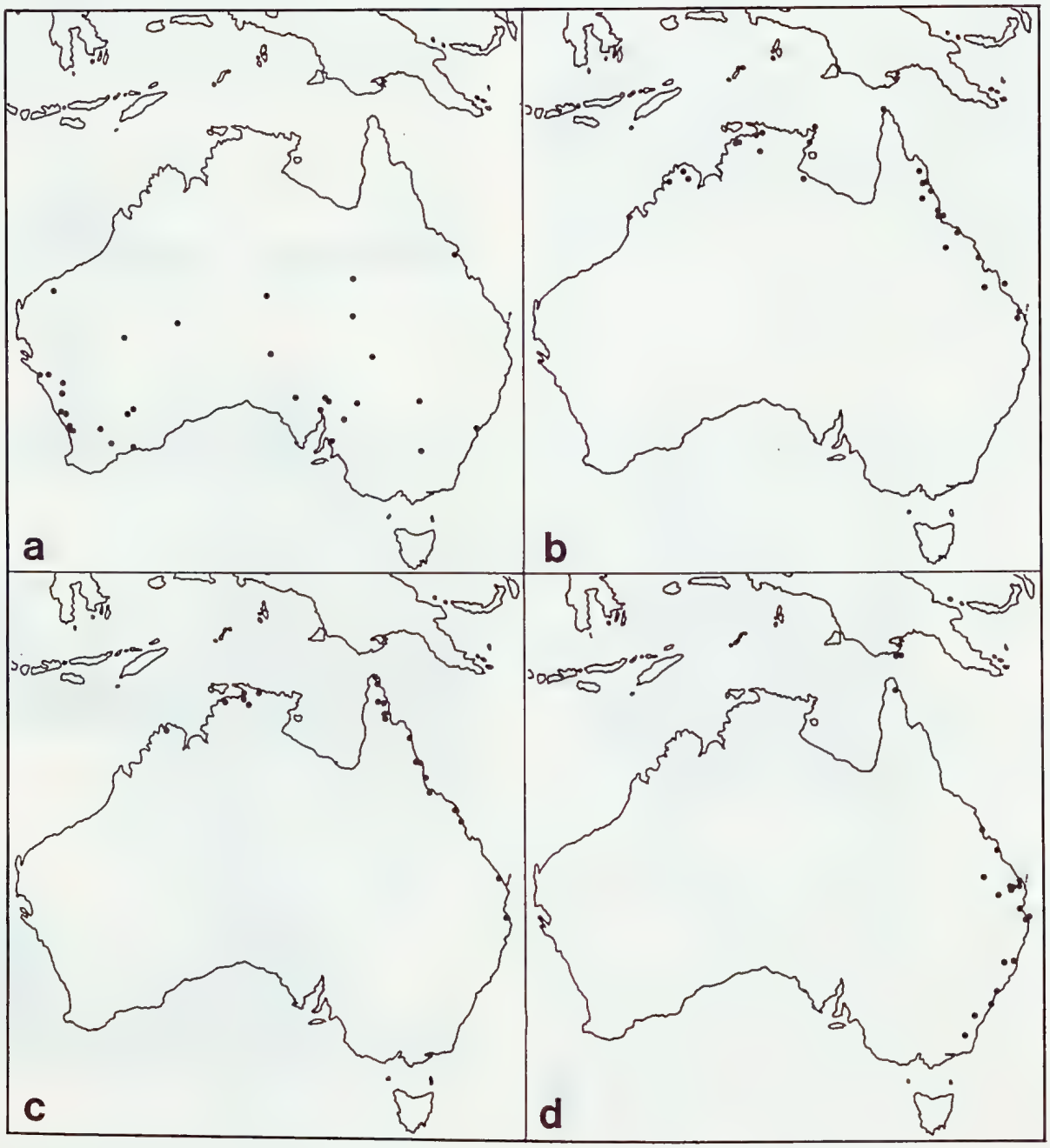


**Fig.6.** Distribution maps – a, *I. australiensis*; b, *I. dubitorius*; c, *I. proficiscator*; d, *I. rufus*.

Vein 1-SR+M straight. Vein 3-CU1 not expanded posteriorly. Vein cu-a interstitial. Hindwing vein ratio = 1.1. Apex of vein C+SC+R with 4 to 6 thickened setae. Fore leg ratio = 1.0:1.05:1.45. Hind leg ratio = 1.85:2.64:1.0. Hind basitarsal index = 5.0. First metasomal tergite 1.28 times longer than apically wide, without sculpture apart from a few small punctures at the bases of setae. Second tergite approximately 2.3 times wider than medially long. Second suture sinuous and coarsely crenulate. Third to fifth tergites with smooth, transverse, subposterior grooves. Fourth and fifth tergites with crenulate, transverse, sub-basal grooves. Ovipositor, (exserted part) approximately 1.4 times longer than syntergite 2 + 3; maximum depth approximately 0.7 times diameter of basal flagellomeres. Yellow to pale orange-yellow except for the following which are black: antennae, head (except for labiomaxillary complex and palps) mesoscutum, posterior three quarters of the mesopleuron + mesosternum, metasternum, propodeum (except for a medio-posterior mark and a narrow posterior margin), metasomal tergites 5-7, hind femur (excluding trochantellus) distal half of hind tibia, hind tarsus, and ovipositor sheaths. Wings pale yellow except for the apical third which is brown and a narrow transverse band on the forewing at the level of the parastigma.

*Male*. Generally smaller than females but otherwise similar. Genitalia with an elongate but not medially produced basal ring. Parameres with a band of setae extending around the apex to approximately half way along the ventral edge. Volsellae narrowly setose medially. Digitus weakly concave dorsally, with small, apical tooth-like process.

**Notes.** *Iphiaulax dubitorius* appears to have a rather northern distribution with few records from far inland (Fig.6b) and collection dates indicate that it may have two main periods of abundance, one around May and June and a second around November and December (Fig.5d).

### *Iphiaulax innotatus* (Turner) n.comb.

Fig.1b

*Cyanopterus innotatus* Turner, 1918: 95.–Parrott, 1953: 206.–Shenefelt, 1978: 1680.

**Material examined.** HOLOTYPE female labelled "*Cyanopterus innotatus* Type Turn.", "B.M.TYPE HYM. 3.c 584", "Cairns, Kur. 1.02" & "1909-45" (BMNH; 3.c 584).

Queensland: 1 female, Dunk Island, Aug. 1927 (QM); 3 females, Dunk Island, Aug. 1927 (QU); 2 females, Redlynch, Sept. 1938 (BMNH).

**Description.** *Female*. Length of body 8-11 mm, of forewing 9-11.5 mm and of ovipositor (part exserted beyond the apex of the metasoma) 4.5-5.5 mm. Antennae with approximately 90 flagellomeres. Terminal flagellomere strongly acuminate. Tentorial ratio = 1.0:3.7:2.2. Face rather densely setose except medially, smooth and shiny between the small punctures at the bases of the setae. Facial ratio = 1.0:2.0:1.0. Frons glabrous, broadly, shallowly impressed with a deep midlongitudinal sulcus. Ocellar ratio = 1.2:1.0:3.0. Mesosoma 1.66 times longer than high. Notauli weekly impressed at anterior of mesoscutum. Scutellar sulcus with numerous fine transverse carinae. Propodeum sparsely long setose medially, more densely so laterally. Radial sector ratio = 4.5:3.3:1.0. Submarginal cell ratio = 1.19:2.41:1.0. Pterostigmal index = 3.0. = Vein 3-CU1 not expanded posteriorly. Vein cu-a marginally postfurcal, straight. Hindwing vein ratio = 1.0:1.0. Apex of vein C+SC+R with 5 thickened setae. Fore leg ratio = 1.0:1.03:1.45. Hind leg ratio = 1.9:2.8:1.0. Hind basitarsal index = 5.2. Metasoma smooth and shiny. First metasomal tergite 1.58 times longer than maximally wide; without sculpture. Second tergite approximately 2.4 times wider than medially long. Second suture sinuous, without sculpture. Posterior margin of third to fifth tergites with a smooth, narrow, transverse subposterior groove, that of the third tergite being weaker. Ovipositor approximately 3 times longer than syntergite 2+3; maximum depth approximately equal to diameter of basal flagellomeres. Dull orange-red (the metasoma somewhat more yellow), except antennae and head (excluding palps), hind tarsi and ovipositor sheaths which are black. Wings medium to dark brown, basal three quarters of pterostigma yellow and a posteriorly narrowing area below this nearly clear.

*Male*. Unknown.

**Notes.** The few specimens of this species indicate that it may be restricted to North Queensland, and in particular, its offshore islands. No specimens from outside of Australia that can be unambiguously assigned to this species have been seen, though similar species are found in Papua New Guinea.

### *Iphiaulax latistigma* n.sp.

Fig.1a

**Material examined.** HOLOTYPE female labelled "Guadalcanal I. 1.27-31 Sol.Is.", "J.A.Kusche Coll" & "Collection of W.M. Giffard" (BMH). [Left forewing detached]. PARATYPES: 1 female, labelled "Cairns. Q. 9-20", "J.A. Kusche Coll" & "Collection of W.M. Giffard" [Left forewing missing] (BMH). 1 female labelled "SOLOMON Is. Guadalcanal, Lunga May-June 1935 R.A. Lever" (QC, ex-BMNH).

**Additional material** (not included in paratype series). Solomons: 1 female, Lavoro Plantation, Guadalcanal Island, – 26.-27 (AM); 1 male, Lunga, Guadalcanal Island, no date (BMNH).

**Description.** *Female.* Length of body 11.5-12.5 mm, of forewing 12.5-13.8 mm and ovipositor (part extending beyond apex of the metasoma) 3.8-5.5 mm. Face moderately setose with punctate sculpture superimposed on a coriaceous background. Tentorial index = 1.0:3.1:2.0. Facial index = 1.0:2.1:1.1. Frons glabrous, broadly generally impressed with moderately well-developed midlongitudinal sulcus. Ocellar ratio = 1.0:1.1:2.35. Metasoma approximately 1.78 times longer than high. Scutellar sulcus narrow and crenulate. Propodeum densely setose laterally, sparsely setose medially. Radial sector ratio = 8.07:5.4:1.0. Submarginal cell ratio = 1.0:2.8:1.2. Pterostigmal index approximately 2.0. Vein 1-SR+M more or less straight. Vein cu-a postfurcal. Hind wing vein ratio = 1.0:1.1. Apex of vein C+SC+R with 6-8 especially thickened bristles. Fore leg ratio = 1.0:1.15:1.48. Hind leg ratio = 1.72:2.52:1.0. Hind basitarsal index = 5.3. Metasoma smooth and shiny. First tergite 1.4 times longer than maximally wide, without a median carina. Second tergite approximately 2.6 times longer than maximally wide. Second metasomal suture smooth. Posterior margin of fourth and fifth tergites with a transverse subposterior groove (third tergite sometimes with a trace of a groove). Ovipositor approximately 1.5 times longer than syntergite 2+3; maximum depth 0.7-1.0 times the diameter of the basal flagellomere. Dull orange-red except for the following which are black or piceous red: antenna, head (including labio-maxillary complex but excluding palps), metasoma, hind tibia and tarsus and ovipositor sheaths; the propodeum and metapleuron are sometimes piceous. Palps yellowish brown. Wings medium-brown except for the extreme base which is orangish, the pterostigma which is cream or ivory white and a small area below the pterostigma which is more or less clear.

*Male.* Similar to female but rather smaller.

**Notes.** *Iphiaulax latistigma* n.sp. appears to be one of the common braconines in the Solomon Islands (though previously undescribed) and the colour pattern it displays is characteristic of larger braconines from those islands (see Cameron, 1911) and from the south of Papua New Guinea. It is possible therefore that the data on the BMH specimen (the only one apparently from Australia) is erroneous or, at least, that *I. latistigma* is not endemic to Australia. It is included here in case it does and because it is an undescribed yet obviously common species in the Solomons.

**Etymology.** Name refers to the broad pterostigma.

### *Iphiaulax proficiscator* (Fabricius)

Figs 1e, 5b, 6c

*Ichneumon proficiscator* Fabricius, 1775: 335.–Fabricius, 1781: 428.–Gmelin, 1790: 2689.–Fabricius, 1793: 153.–Zimsen, 1964: 372.
*Ichneumon profisciscator* [*sic.*].–Fabricius, 1787: 264.
*Bracon proficiscator.*–Fabricius, 1804: 105.–Dalla Torre, 1898: 285 [includes old references].–Szépligeti, 1904: 37.
*Cyanopterus profiscator* [*sic.*].–Turner, 1918: 94–95.
*Cyanopterus proficiscator.*–Turner, 1919: 231.–Shenefelt, 1978: 1681.–Parrott, 1953: 207.
*Iphiaulax proficiscator.*–Quicke, 1988c: 201.
*Ichneumon hospitator.*–Fabricius, 1775: 335 n.syn.
*Bracon hospitor* [*sic.*].–Fabricius, 1804: 106.
*Bracon hospitator.*–Dalla Torre, 1898: 272.–Szépligeti, 1904: 37.–Parrott, 1953: 205.–Shenefelt, 1978: 1492.
*Iphiaulax hospitator.*–Quicke n.comb.

**Material examined.** HOLOTYPE female of *proficiscator*, no data (BMNH; Banks Collection). HOLOTYPE male of *hospitator*, no data (BMNH; Banks Collection).

Northern Territory: 1 female, Baroalba Creek, Oct. 1972 (ANIC); 1 male, 1 female, Cahills Crossing, Alligator River, Oct. 1972 (ANIC); 1 female, Coastal Plains Research Stn, Lower Adelaide River, "Pupa in bored-out stem of *Mimosa pigra*. Parasite of cerambycid? Emg. 18. Nov. 1985", Nov. 1985 (ANIC); 2 females, Maningrida, Mar. 1961 (BMH); 1 male, Mudginbary, Nov. 1972 (ANIC); 1 male, Mudginbary, June 1973 (ANIC); 1 female, Port Darwin, no date (BMNH); 1 male, West Alligator Mouth, July 1979 (QM). Queensland: 1 female, Box Creek, Proserpine, no date (AM); 1 female, Cairns, Dec. 1951 (AM); 1 female, Finch's Bay, Cooktown, June 1951 (AM); 2 females, Iron Range, ? 1947 (AM); 1 female, Mount Lamond, Iron Range, Jan. 1972 (AM); 2 females, 4 males, Bundaberg, "in mangroves", Oct. 1977 (ANIC); 1 male, Bundaberg, Oct. 1972 (ANIC); 1 male, Bundaberg, Jan. 1973 (ANIC); 1 male, Bundaberg, Jan. 1978 (ANIC); 1 female, Cape York, Apr. 1902 (ANIC); 1 female, Cape York, May 1902 (BMNH); 1 male, Mount Walsh National Park, Aug. 1977 (ANIC); 1 female, Mount Tozer Area, Apr. 1973 (ANIC); 1 female, Leo Creek Road, McIlwraith Range, "c. 500m", July 1976 (ANIC); 1 female, Stewart River, Coen, June 1976 (ANIC); 1 male, Somerset, Apr. 1973 (ANIC); 2 females, Lockerbie Area, Apr. 1973 (ANIC); 1 male, Gunshot Creek, July 1975 (ANIC); 1 female, Captain Billy Creek, July 1975 (ANIC); 1 male, Pinnacle Creek, 27 km north of Archer Crossing, June 1975 (ANIC); 1 female, Capsize Creek, 64 km north of Archer Crossing, June 1975 (ANIC); 1 female, Iron Range, Apr. 1964 (ANIC); 1 female, Iron Range, May 1971 (ANIC); 4 females, 1 male, Mackay, ? 1909 (BMNH); 2 females, Mackay, May 1934 (QM); 1 female, Kuranda, May-June 1913 (BMNH); 1 female, Sue Island, May 1985 (QC; ex DPIB); 1 female, Dunk Island, May 1914 (QM); 1 male, Townsville, no date (QM); 1 female, Brisbane, May 1951 (QU); 1 male, Brisbane, "in mangrove", Nov. 1957 (QU); 1 female, Brisbane, Sept. 1961 (QU). Western Australia: 1 male, Carson Escarpment, July 1975 (ANIC); 1 male, Drysdale River, July 1975 (ANIC).

**Description.** *Females.* Length of body 10-12 mm, of forewing 9.0-11.8 mm and of ovipositor (part exserted beyond apex of metasoma) 3.5-4.6 mm. Antennae with approximately 90 flagellomeres. First flagellomere 1.43 and 1.5 times longer than the second and third flagellomeres respectively, the latter being 1.2 times wider than long. Tentorial ratio = 1.0:3.53:2.16. Facial ratio

= 1.0:2.1:1.1. Frons deeply broadly impressed with a weak midlongitudinal suture. Ocellar ratio = 1.0:1.4:2.6. Mesosoma approximately 1.6 x longer than high. Scutellar sulcus crenulate. Radial sector ratio = 5.48:4.19:1.0. Submarginal cell ratio = 1.0:2.4:1.2. Pterostigmal index = 2.75-2.85. Vein 1-SR+M virtually straight. Vein 3-CU1 not expanded posteriorly. Vein cu-a interstitial, straight. Hind wing vein ratio = 1.0:1.1. Apex of hindwing vein C+SC+R with 5-7 especially thickened bristles. Fore leg ratio = 1.0:1.08:1.6. Hind leg ratio = 1.8:2.8:1.0. Hind basitarsal index = 4.8. Metasoma smooth and shiny. First metasomal tergite approximately 1.36 times longer than maximally wide; without sculpture. Second tergite approximately 2.4 times wider than medially long. Second suture smooth. Ovipositor approximately 0.4 times forewing length; maximum depth 1.1-1.3 times diameter of basal flagellomeres. Orange-yellow to orange except for the following which are black or piceous: antennae, head (except palps), apex of hind tibia, hind tarsus and ovipositor sheaths. Basal two fifths of forewing yellow, apex brown except for the pterostigma which is yellow and a broad band below the pterostigma which is largely yellow. Basal three fifths of hindwing yellow, remainder brown.

*Male.* Similar to female. Metasomal tergites 6 and 7 often somewhat piceous.

**Notes.** This species appears to have a principally northern and north-eastern coastal distribution (Fig.6c) and collection data histograms indicate two periods of abundance, the first from April to July and a second around the October–November period (Fig.5b).

### *Iphiaulax rufus* Szépligeti

Figs 1d, 2c, 5c, 6d

*Iphiaulax rufus* Szépligeti, 1901: 397.–Szépligeti, 1904: 23.–Szépligeti, 1905: 35.
*Cyanopterus rufus*.–Szépligeti, 1906: 586.–Turner, 1918: 231.–Tillyard, 1926: 269.–Parrott, 1953: 207.–Shenefelt, 1978: 1681.

**Material examined.** HOLOTYPE female, labelled "*I. rufus* det. Szépligeti", "Holotype female *Iphiaulax rufus* Szépl. 1901, Papp '69", "Hym. Typ. No. 1207 Mus. Budapest" (HNHM).

New South Wales: 1 female, Cowan, Sydney, Feb. 1947 (AM); 1 female, Coal & Candle Creek, Jan. 1946 (AM); 1 female, Mount Tomah, Jan. 1978 (AM); 2 females, Bilpin, Jan. 1978 (AM); 1 male, 1 female, Lorien Wild, Jan. 1987 (AM); 1 male, Wollombi, Ebor District, Mar. 1987 (AM); 1 female, Manly, Dec. 1907 (AM); 1 female, Harrington, Jan. 1986 (AM); 1 female, Crowdy Head, "Ex *Acacia saphonae* on beach hind dune zone", Sept. 1985 (AM); 1 female, Maitland Bay, Jan. 1988 (AM); 1 female, Narrabeen, Feb. 1936 (ANIC); 1 male, 1 female, Sawtell, Apr. 1968 (ANIC); 1 female, Greta, ? 1951 (BMH). Queensland: 1 female, Carnarvon Range, Dec. 1934 (AM); 1 female, Yeppoon, Oct. 1924 (AM); 1 male, Yeppoon, Oct. 1924 (QM); 1 female, Miles, Jan. 1939 (AM); 1 female, Murray Island, Torres Strait, no date (AM); 1 female, Claudie River, near Mount Lamond, June 1986 (AM); 1 male, Dauan Island, Torres Strait, June 1962 (ANIC); 1 female, Saibai Island, Torres Strait, June 1962 (ANIC); 1 male, Mount Walsh National Park, Jan. 1973 (ANIC); 1 female, Mount Walsh National Park, June 1977 (ANIC); 1 female, 3 males Mount Walsh National Park, Jan. 1978 (ANIC); 1 female, Mount Walsh National Park, Feb. 1979 (ANIC); 1 male, Cordalba State Forest, 29 km south-west of Bundaberg, Oct. 1978 (ANIC); 3 females, Cordalba State Forest, 29 km south-west Bundaberg, Dec. 1979 (ANIC); 1 female, 2 males, Degilbo, Dec. 1978 (ANIC); 1 female, Coast Range, Biggenden, Aug. 1974 (ANIC); 1 female, Coast Range, Biggenden, Feb. 1978 (ANIC); 1 female, Coast Range, Biggenden, Oct. 1979 (ANIC); 1 female, Baldwin Swamp, Bundaberg, Oct. 1977 (ANIC); 1 male, Bundaberg, May 1960 (QC); 1 female, Bundaberg, "in mangroves", Oct. 1977 (ANIC); 1 (sex unknown; metasoma missing), Pine Creek, Bundaberg, no data (ANIC); 2 females, Mundabbera, Apr. 1957 (ANIC); 1 male, Captain Billy Creek, Cape York Peninsula, July 1975 (ANIC); 2 males, Hogback Range, Mar. 1973 (ANIC); 2 males, Bla Bla Range, Dec. 1974 (ANIC); 1 female, Rockpool Gorge, Mar. 1975 (ANIC); 1 female, Summit Mount Walsh, "c. 1000m", Nov. 1976 (ANIC); 1 male, Isis District, near Childress, Sept. 1973 (ANIC); 1 male, Ban Ban Range, Jan. 1974 (ANIC); 1 female, Mount Tozer Area, Apr. 1973 (ANIC); 1 female, Burnett River, Bundaberg, Jan. 1976 (ANIC); 1 male, Burnett River, Bundaberg, Nov. 1976 (ANIC); 1 male, Electra State Forest, Nov. 1976 (ANIC); 1 female, Electra State Forest, Dec. 1976 (ANIC); 1 female, Electra State Forest, Jan. 1977 (ANIC); 1 male, Electra State Forest, Apr. 1977 (ANIC); 2 females, 4 males, Mackay, no date (BMNH); 1 male, Brisbane, May 1909 (QM); 1 female, Brisbane, Dec. 1912 (QM); 1 female, Brisbane, Feb. 1916 (QM); 1 female, Brisbane, Aug. 1923 (QC); 1 female, Stradbroke Island, Sept. 1915 (QC); 1 male, Caloundra, Oct. 1912 (QM).

New Zealand: 1 female, Hunter River, no date (BMNH).

**Description.** *Female.* Length of body 9.0-12.5 mm, of forewing 9.5-13.5 mm and of ovipositor (part exserted beyond apex of metasoma) 4.0-5.5 mm. Antenna with approximately 100 flagellomeres. Tentorial ratio = 1.0:3.2:2.6. Face moderately densely long setose with distinct punctures at the bases of the setae, coriaceous between these punctures. Facial ratio = 1.0:1.92:1.0. Frons glabrous, moderately deeply impressed behind the antennal sockets with a weak midlongitudinal sulcus. Ocellar ratio = 1.0:1.58:3.55. Mesosoma approximately 1.74 times longer than maximally deep. Notauli almost totally absent. Scutellar sulcus narrow and finely crenulate. Propodeum sparsely long setose medially, densely so laterally. Radial sector ratio = 6.21:4.55:1.0. Submarginal cell ratio = 1.0:2.54:1.0. Pterostigmal index = 2.65. Vein 1-SR+M weakly angled posteriorly shortly after arising from vein 1-SR. Vein cu-a interstitial, evenly curved. Hind wing vein ratio = 1.08:1.0. Apex of hindwing vein C+SC+R with 3 to 6 thickened bristles. Fore leg ratio = 1.0:1.8:1.57. Hind leg ratio = 1.82:2.7:1.0. Hind basitarsal index = 6.3. First metasomal tergite approximately 1.15

times longer than maximally wide; without sculpture. Second tergite 2.2-2.4 times wider than medially long. Second suture sinuous and smooth. Third tergite with at most a weak smooth, transverse, subposterior groove medially. Tergites 4 and 5 with well-developed, smooth, transverse, sub-posterior grooves. Ovipositor (exserted part) approximately 2 times longer than syntergite 2 + 3; maximum depth (preapical) 1.41-1.58 times width of basal flagellomeres. Orange-red (metasoma sometimes somewhat darker), antennae, head, apical 0.2-0.4 of hind tibia, hind tarsus and ovipositor sheaths black. Wings with basal 0.4-0.5 yellow, apical part grey-brown to brown except for the pterostigma (except apex) which is yellow, and a small area below this which is clear.

*Male*. Similar to female, wings sometimes more palely marked.

**Notes.** *Iphiaulax rufus* has a principally south-eastern distribution most records being from New South Wales and southern Queensland though a few apparently conspecific individuals have been collected in north Queensland and its off-shore islands (Fig.6d); the record from Hunter River may possibly refer to a locality outside of New Zealand as the country was not specified. Flight activity appears to peak around December and January (Fig.5c).

## Species Referrable to Other Genera

### *Iphiaulax rubricepsis* Shenefelt

*Iphiaulax rubriceps* Froggatt, 1916: 564 (non Brethes, 1913: 57).
*Iphiaulax rubricepsis* Shenefelt, 1978: 1692 [replacement name].

**Comments.** It is clear from the illustrated original description that this species belongs to the doryctine genus *Syngaster* Brullé, hence *Syngaster rubricepsis* n.comb.

### *Iphiaulax trinotata* Ashmead

*Iphiaulax trinotata* Ashmead, 1900: 359.

**Comments.** I have examined the holotype male of this species which is in the USNM (type No. 4917) and found it to belong to the genus *Bracon* to which it is hereby transfered, hence *Bracon trinotata* (Ashmead) n.comb.

### *Chaoilta* Cameron

*Chaoilta* Cameron, 1899: 80.
*Platybracon* Szépligeti, 1900: 49 (*Platybracon depressus* Szépligeti, 1900, monotypy); synonymised by Roman, 1913.
*Blastomorpha* Szépligeti, 1900: 50 (*Blastomorpha decorata* Szépligeti, 1900, subsequent designation of Viereck, 1914); synonymised by Quicke, 1981.
*Iphioilta* Ramakrishna Ayyar, 1928: 60d (*Iphioilta malabarica* Ramakrishna Ayyar, 1928, original designation); synonymised by Quicke, 1987 on the authority of C. van Achterberg.

**Type species.** *Chaoilta lammellata* Cameron, 1899, monotypy.

**Description.** *Female*. Medium to large braconine wasps. Median flagellomeres longer than wide. Basal 1-3 flagellomeres with especially long setae ventrally. Pedicellus petiolate. Scapus highly modified, apicomedial margin with separate large and small concave areas, basally concavely pedicellate. Face with a more or less strongly produced, transverse ledge, with (subgenus *Blastomorpha*) or without (subgenus *Chaoilta*) medial horn-like and distally concave projection above this. Eyes glabrous. Frons broadly impressed. Head elongate (cubicoid). Mesosoma usually more or less strongly dorsoventrally compressed. Forewing vein r-m with 2 bullae. Apex of hindwing vein C+SC+R with 1 especially thickened bristle. Base of hindwing with glabrous area distal to vein cu-a. Fore tarsus at least 1.6 times longer than fore femur (excluding trochantellus). Apicoventral setae of penultimate tarsal article very elongate, extending at least 0.9 of ventral length of telotarsus (excluding claw). Hind femur and tibia with numerous long setae ventrally as well as many shorter ones. First metasomal tergite with wide, flat lateral areas. Second metasomal tergite with well-developed pair of posteriorly diverging grooves and with distinct, acute, striate, midbasal triangular area. Metasomal tergites 3-5 with anterolateral, posteriorly diverging grooves. Ovipositor shorter than forewing; with preapical dorsal nodus and apicoventral serrations.

*Male*. As for females except facial protuberance usually less well developed, and apicoventral tarsal bristles not so elongate. With pair of large sac-like intertergal glands between seventh and eighth abdominal tergites and with pair of tubular glands opening at pore on eighth abdominal (seventh metasomal) tergite close to its anterolateral corners (Quicke, in press). Rectum fused to eighth abdominal tergite.

**Notes.** The genus *Blastomorpha* was erected by Szépligeti (1900) for those species which possess a horn-like process above the facial lamellum. Although in *Chaoilta sensu stricto* there is often a more or less protruding, mid-longitudinal ridge running along the facial lamellum, the condition in *Blastomorpha* species is distinct in that the horn-like process is not a simple projection of the carina but has a distinct concave apical area. The author has seen several species with this modification and therefore considers that these should be recognised as belonging to a separate subgenus, *Chaoilta* (*Blastomorpha*) n.stat. to distinguish them from

those species with only a simple cariniform protruberance, *Chaoilta* (*Chaoilta*).

**Biology.** *Chaoilta* belongs to the *Atanycolus* group of genera (Quicke, 1987), members of which have most frequently been reared from beetle larvae which bore just under tree bark, notably species of Buprestidae. Unfortunately there are no host records for Australian species of *Chaoilta* but one Indo-Australian species has been recorded from "large bark-boring beetle larvae" (Quicke, 1988b), indicating that beetle larvae such as Buprestidae are the probable hosts.

## Key to Australian Species of *Chaoilta*

1. Face with a horn-like structure above the protruding transverse lamella (Fig.7a,b); metasomal tergites all black; pronotum strongly emarginate medioanteriorly (Fig.7c) ..... *C.* (*Blastomorpha*) *decorata*

—— Facial lamella at most with a midlongitudinal carina dorsally (Figs 7d, 8a,b); metasomal tergites 1-4 brownish yellow to brownish orange, tergites 5-7 yellow brown or black; pronotum less strongly emarginate medioanteriorly (Figs 7f, 8h) (*C.* (*Chaoilta*)) ..... 2

2. Mesoscutum, scutellum, mesosternum, mid and hind coxae, trochanters and femora largely black; fourth metasomal tergite largely without sculpture (Fig.8f); posterodorsal part of pronotum sparsely setose (Fig.7g) ..... *C. hollowayi* n.sp.

—— Mesoscutum, scutellum, mesosternum, mid and hind coxae, trochanters and femora entirely brownish yellow; fourth metasomal tergite extensively longitudinally striate (Fig. 8a,b); posterodorsal part of pronotum more extensively setose (Fig.8e,g) ..... 3

3. Head black; hind tarsus black except for extreme base ..... *C. nigriceps*

—— Head and hind tarsus (except for telotarsus) brownish yellow ..... 4

4. Wing membrane brown except for clear and yellow markings posterior to pterostigma (Fig.8d) ..... *C. insularis*

—— Wing membrane yellow for at least basal half of median and submedian cells of forewing (see Fig. 8c) ..... *C. lutea*

### *Chaoilta* (*Blastomorpha*) *decorata* (Szépligeti)

Fig.7a–c

*Blastomorpha decorata* Szépligeti, 1900: 50.–Kohl, 1907: 290.
*Chaoilta decorata*.–Szépligeti, 1904: 17.–Turner, 1917: 241.–Shenefelt, 1978: 1667.

**Material examined.** HOLOTYPE female from Papua New Guinea labelled "Mafor Fruhstorfer", "H. Type No 850. Museum Budapest" (HNHM).

Queensland: 3 females, Claudie River 5 km west of Mount Lamond, Jan. 1972 (AM); 1 (sex unknown, metasoma missing), Cooktown, Nov. 1904 (BMNH); 1 female, Gordon Creek area, Claudie River district, July 1982 (QU); 2 females, Iron Range, June 1971 (ANIC); 1 female, Iron Range, Apr.–May 1973 (ANIC); 1 female, Iron Range, Mar. 1975 (DPIB); 2 females, Iron Range, June–July 1981 (ANIC); 2 females, McIvor River Crossing, 40 km north of Cooktown, Aug. 1976 (ANIC); 1 male, Mount Tozer near Iron Range National Park, June–July 1986 (ANIC).

Papua New Guinea: 1 female, Bulolo, 700 m, Nov. 1957 (BMH); 2 females, Bulolo River, 700 m, Feb. 1969

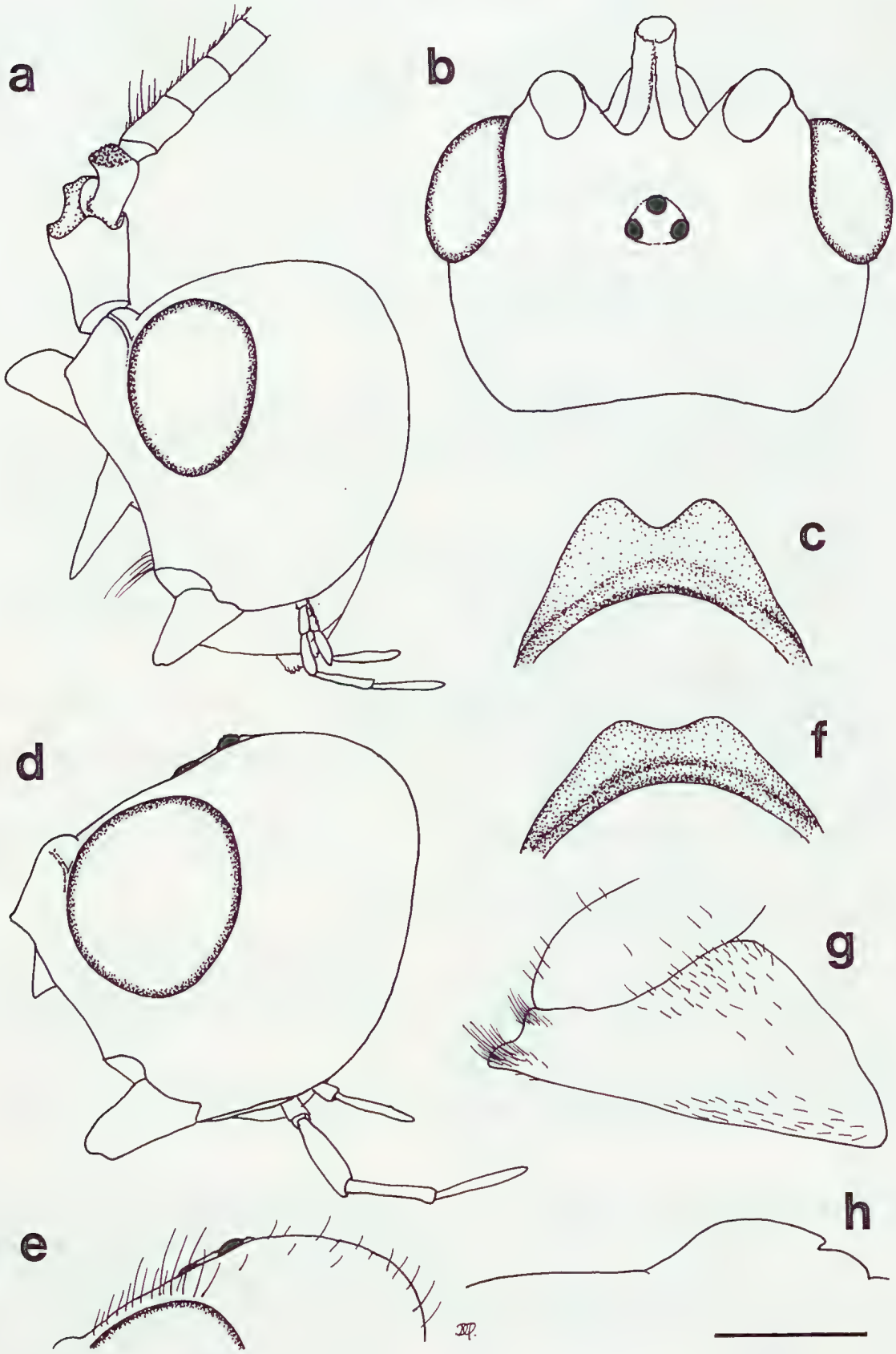


**Fig.7.** a–c, *Chaoilta* (*Blastomorpha*) *decorata*: a, head and base of antenna, lateral aspect; b, head, dorsal aspect; c, pronotum, dorsal aspect. d–h, *Chaoilta* (*Chaoilta*) *hollowayi* n.sp.: d, head, lateral aspect; e, top of head showing long setae at edge of frons; f, pronotum, dorsal aspect; g, pronotum, lateral aspect; h, scutellum, left profile. Scale bar: a,b, 1.0 mm; c,g, 0.75 mm; d–f, 0.5 mm; h, 0.4 mm.

(BMH); 1 female, Green River/Sepik River Junction, 200 m, June 1963 (BMH); 1 female, north-east of Garaina, 550-750 m, Jan. 1968 (BMH); 3 females, Kiunga, Fly River, Aug. 1957 (BMH); 3 females, Kiunga, Fly River, 35 m, Aug. 1969 (BMH); 1 female, Kuper Range, 25 km south-east of Salamaua, Jan. 1969 (BMH); 1 female, Popondetta, June 1966, "light trap" (BMH).

No data: 1 female, (QM).

**Description.** *Female*. Length of body 12-18 mm, of forewing 11-16 mm, and of ovipositor (exserted part) 14-21 mm. Antennae with approximately 60 flagellomeres. Basal 3 flagellomeres with long apicoventral setae. First flagellomere 1.13 and 1.3 times longer than the second and third respectively, the latter being 1.18 times longer than wide. Inter-tentorial distance: tentorio-ocular distance = 1.0 : 1.16-1.17. Face with an extremely strong, distinctly down-curved, plate-like protuberance and with long, apically obtuse, horn-like process above this. Frons extensively sparsely short setose. Ocellar ratio = 1.0:1.0:5.7. Head index = 0.82-1.04. Mesosoma approximately 2.15 times longer than high. Pronotum strongly emarginate medioanteriorly in dorsal aspect; posterodorsally extensively, moderately-densely setose. Scutellar sulcus finely crenulate. Propodeum without striations; smooth and shiny. Radial sector ratio = 5.8:5.6:1.0. Submarginal cell ratio = 1.0:2.47:1.0. Vein 1-SR+M moderately strongly curved posteriorly. Hindwing-hindwing vein ratio = 1.4:1.0. Fore leg ratio = 1.0:1.1:2.0. Fore basitarsal index = 6.5. Hind leg ratio = 1.36:2.27:1.0. Hind basitarsal index = 5.7. Metasoma moderately strongly sculptured basally, smooth but densely setose apically. First tergite slightly longer than maximally wide, the lateral areas longitudinally striate, the raised median area striate to foveate posteriorly. Second tergite 2 times wider than medially long; longitudinally striate medially, confused striate-rugose laterally. Third tergite at most striate basally, remainder of tergite and subsequent ones smooth but densely setose and with distinct punctures at bases of setae. Ovipositor approximately 1.35 times length of forewing. Orange-red to brown-red, except head which is yellow and flagellum, hind tibia and tarsus, metasoma and ovipositor sheaths which are black. Wings dark brown except for pterostigma which is yellow and flexion line between apex of parastigma and base of second subdiscal cell which is clear.

*Male*. Very similar to female.

**Notes.** This species is common in Papua New Guinea and North Queensland.

### *Chaoilta* (*Chaoilta*) *hollowayi* n.sp.

Figs 7d–h, 8f

**Material examined.** HOLOTYPE female labelled "North Slope, Bluff Ra., Biggenden, Qld, 10 May 1973 H. Frauca" (ANIC). PARATYPES – New South Wales: 2 males, 2 females, Baradine, May 1954 (ANIC); 1 male, Mount Harris, Sept. 1982 (AM). Queensland: 1 female, Amby, Nov. 1979 (QU); 1 female, Cunnamulla, Apr. 1942 (AM); 1 female, Duaringa District, Jan. 1940 (AM); 1 female, no locality or date (AM). Western Australia: 1 female, Beverley, Mar. 1914 (ANIC); 1 female, Cadoux, Oct. 1981 (WAM).

**Description.** *Female*. Length of body 7.5-9.5 mm, of forewing 8.5-9.0 mm, of antennae 7.7-8.25 mm and of ovipositor (part exserted beyond apex of metasoma) 7.5-8.0 mm. Antennae with 51 flagellomeres. First flagellomere 1.27 and 1.18 times longer than second and third respectively, latter being 1.5 times longer than wide. Inter-tentorial distance: tentorio-ocular distance = 1.2:1.0. Face with a moderately developed transverse protrusion. Dorsal side of protrusion with a midlongitudinal carina bordered by crenulae. Facial ratio = 1.22:2.28:1.0. Frons largely glabrous except for 2 rows of rather long setae close to eye. Ocellar ratio = 1.7:1.0:5.3. Head index = 0.88-1.1. Mesosoma 2.0-2.6 times longer than high. Pronotum only weakly emarginate apicomedially; sparsely setose posterodorsally. Scutellum usually rather strongly arched in profile (less so in more dorsoventrally compressed specimens). Propodeum smooth or finely, longitudinally striate medio-posteriorly. Radial sector ratio = 6.8:4.25:1.0. Submarginal cell ratio = 1.0:2.47:1.0. Hindwing vein ratio = 1.0:1.8. Fore leg ratio = 1.05:1.0:1.67. Fore basitarsal index = 6.5. Hind leg ratio = 1.43:2.32:1.0. Hind basitarsal index = 6.3. Metasoma largely with confused longitudinal striation anteriorly, smooth posteriorly. First tergite marginally longer than posteriorly wide; lateral areas smooth, raised medium area largely longitudinally striate. Second tergite 2.6-2.8 times wider than medially long. Second and third tergites largely longitudinally striate. Fourth and subsequent tergites smooth except for some microsculpture and the crenulate, transverse, subposterior grooves; moderately setose. Ovipositor approximately 0.8 times length of forewing. Ochreous yellow except for the following which are black or piceous brown: antennae, tips of mandibles, stemmaticum, posterior part of pronotum, mesothorax, metanotum, part of metapleuron, coxae, trochanters, variable amounts of femora, apex of hind tibia, hind tarsus, metasomal tergites 5-7, metasomal sternites and hypopygium, ovipositor sheaths. Posterior margin of tergite 6 white. Basal third of wings yellow, apical two thirds grey-brown to dark brown except for the pterostigma which is yellow.

**Etymology.** Named in honour of Geoff Holloway.

**Notes.** An entirely Australian species known so far from New South Wales, Queensland and Western Australia.

### *Chaoilta* (*Chaoilta*) *insularis* (Cameron)

Fig.8d,e

*Platybracon insularis* Cameron, 1911b: 353.–Brues, 1918:

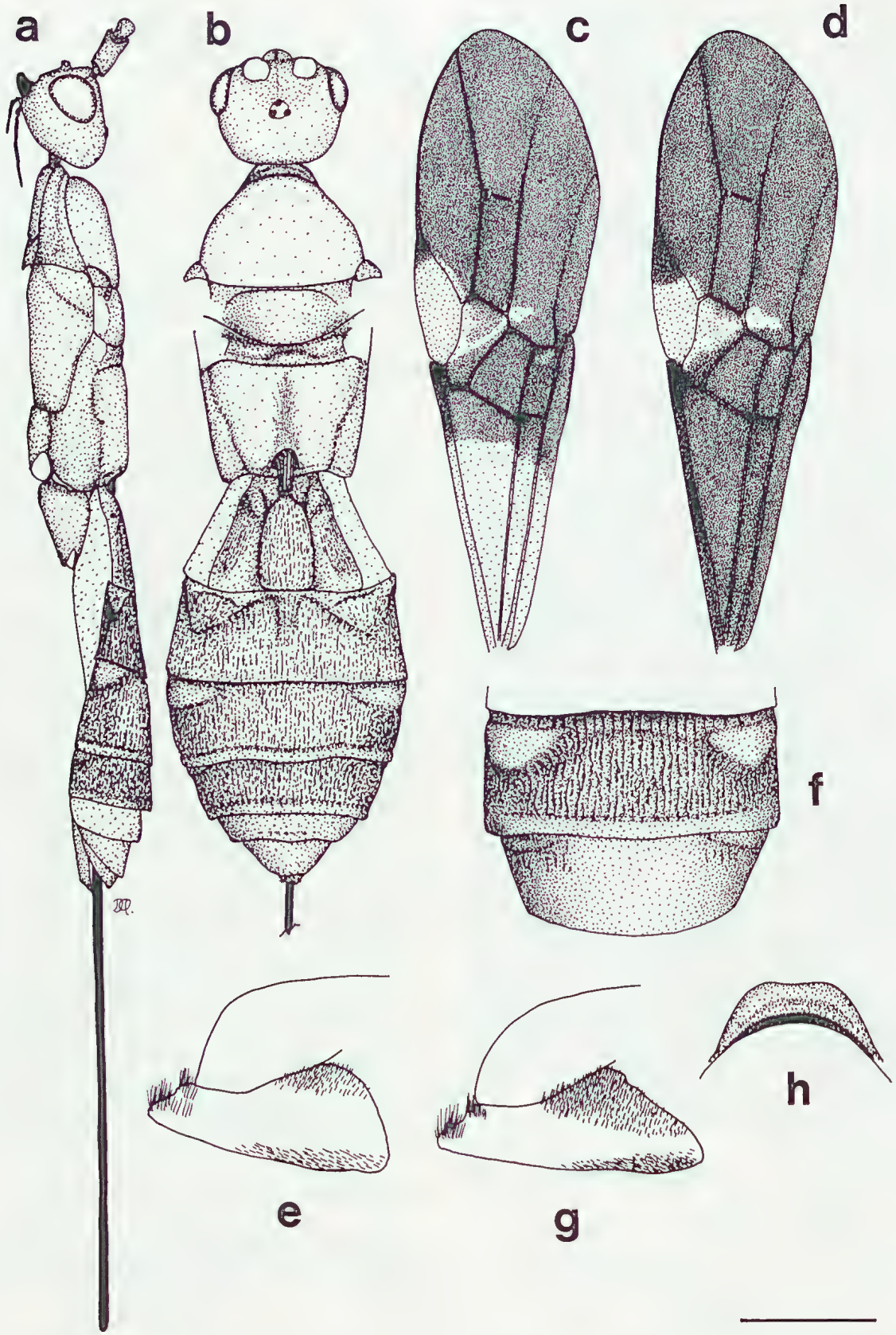


**Fig.8.** a–c, *Chaoilta* (*Chaoilta*) *nigriceps*: a, habitus, lateral aspect; b, habitus, dorsal aspect; c, right forewing, showing colour pattern. d,e, *Chaoilta* (*C.*) *insularis*: d, right forewing showing colour pattern; e, pronotum, lateral aspect. f, *Chaoilta* (*C.*) *hollowayi* n.sp., metasomal tergites 3 and 4. g,h, *Chaoilta* (*C.*) *lutea*: g, pronotum, lateral aspect; h, pronotum, dorsal aspect. Scale bar: a,b, 2.0 mm; c,d, 2.5 mm; e,g,h 0.9 mm; f, 1.15 mm.

106.
*Chaoilta insularis*.–Baltazar, 1972: 263.–Shenefelt, 1978: 1668.

**Material examined.** HOLOTYPE female labelled "*Chaoilta insularis* Cam. type Solomon Islands" (BMNH; 3.c.610).

Queensland: 2 female, Kuranda, Dec. 1951 (AM); 1 female, Kuranda, Nov. 1952 (ANIC); 1 female, Lockerbie Area, Apr. 1973 (ANIC); 1 female, Mareeba, Dec. 1952 (AM).

**Description.** *Female*. Length of body 8.5-12.0 mm, of forewing 8.5-11.5 mm, and of ovipositor (part exserted beyond apex of metasoma) 5.6-7.3 mm. Antenna with 47-53 flagellomeres. First flagellomere 1.33 and 1.5 times longer than the second and third respectively, the latter being 1.6 times longer than wide. Inter-tentorial distance: tentorio-ocular distance = 1.23:1.0. Face with a moderately well-developed transverse protrusion; dorsal side of protrusion with a midlongitudinal carina. Facial ratio = 1.1:2.2:1.0. Frons rather strongly depressed behind the antennal sockets; broadly with short setosity, and with longer setae close to eye. Ocellar ratio = 1.0:1.05:4.35. Head index = 1.4-1.52. Mesosoma 2.55-3.5 times longer than high. Pronotum weakly emarginate apicomedially; with a moderately extensive, densely setose area posterodorsally. Scutellar sulcus finely crenulate. Scutellum more or less flat in profile. Propodeum at least with a crenulate posterior margin, usually with a mediolongitudinal, striate band. Radial sector ratio = 7.0:5.5:1.0. Submarginal cell ratio = 1.0:2.7:1.1. Hindwing vein ratio = 1.0:1.47. Fore leg ratio = 1.0:1.05:1.91. Fore basitarsal index = 6.5. Hind leg ratio = 1.45:2.2:1.0. Hind basitarsal index = 6.0. First metasomal tergite 1.1 times wider than maximally long; lateral areas longitudinally striate at least laterally, raised median area longitudinally striate. Second tergite approximately 3.3 times wider than medially long, with a well-defined striate, midbasal, fusiform area; largely with rugose to striate-rugose sculpture. Third and fourth tergites largely with rugose sculpture; subsequent tergites smooth. Ovipositor (exserted part) approximately 0.6 times length of forewing. Brownish yellow to brownish orange (the head sometimes paler yellow) except for the antennae and ovipositor sheaths which are black. Wings grey-brown; basal three quarters of pterostigma yellow.

**Notes.** Although originally described from the Solomons, the specimens reported here from Australia and Papua New Guinea are apparently conspecific. This species is very close to *C. depressa*.

### *Chaoilta* (*Chaoilta*) *lutea* Cameron

Fig.8g,h

*Chaolta* [*sic*] *lutea* Cameron, 1905a: 102.
*Chaoilta lutea*.–Cameron, 1905b: 42.–Baltazar, 1972: 264.–Shenefelt, 1978: 1668.

**Material examined.** HOLOTYPE female labelled "*Chaoilta lutea* Cam. type. Borneo", "B.M. TYPE HYM. 3.c.594" and "Cameron Coll. 1906-138" (BMNH).

Queensland: 1 female, Iron Range, June 1971 (ANIC); 1 female, Middle Claudie River, Iron Range, Oct. 1974 (AM).

**Description.** *Female*. Length of body 10.5-11.5 mm, of forewing 10.0-11.0 mm and of ovipositor (part exserted beyond to apex of the metasoma) 8.0-8.5 mm. Antennae with 58-61 flagellomeres. First flagellomere 1.1 and 1.25 times longer than the second and third respectively, the latter being 1.25 times longer than wide. Inter-tentorial distance : tentorio-ocular distance = 1.3:1.0. Face with a very well-developed protrusion; dorsal side of protrusion with a midlongitudinal carina. Facial ratio = 1.19:2.32:1.0. Frons with a row of long setae close to eye and with broad moderately setose zone laterally. Ocellar ratio = 1.1:1.0:4.0. Head index = 0.7. Mesosoma 2.5-3.4 times longer than deep. Pronotum weakly emarginate medioanteriorly; extensively densely setose posterodorsally. Scutellar sulcus crenulate. Radial sector ratio = 6.8:5.25:1.0. Submarginal cell ratio = 1.0:2.5:1.05. Hindwing vein ratio = 1.0:1.42. Fore leg ratio = 1.0:1.06:1.9. Fore basitarsal index = 6.3. Hind leg ratio = 1.4:2.3:1.0. Hind basitarsal index 4.9; hind basitarsus tapering gradually from base to apex. Metasoma largely with confused striate sculpture. First tergite about as long as wide; medial and lateral areas with some longitudinal striae. Second tergite approximately 3.3 times wider than medially long, with a raised, elongate, striate midlongitudinal area. Tergites 2-4 largely with confused longitudinal striations. Tergites 5-8 smooth. Ovipositor (exserted part) approximately 0.75 times length of forewing. Ochreous yellow to pale brownish orange (the head sometimes paler yellow) except for the following which are black or piceous: antennae, stemmaticum, hind telotarsi and ovipositor sheaths. Basal third of wings yellow, remainder dark grey-brown or brown except basal two thirds of pterostigma which are yellow and a small area below the pterostigma which is clear.

**Notes.** Widespread Indo-Australian species with just a few Australian specimens known.

### *Chaoilta* (*Chaoilta*) *nigriceps* (Cameron)

Fig.8a–c

*Platybracon nigriceps* Cameron, 1911a: 338.–Parrott, 1953: 209.
*Chaoilta nigriceps*.–Baltazar, 1972: 263.–Shenefelt, 1978: 1669.

**Material examined.** HOLOTYPE female labelled "*Platybracon nigriceps* Cam. Type. NSW.", "B.M. Type Hym. 3.c.609", "Gin Gin, W.W.F. 13.10.01." and "P.

Cameron Coll. 1914-110" (BMNH; 3.c.609).

Northern Territory: 1 female, McArthur River, 48 km south-west by south of Borroloola, Oct. 1975 (ANIC). Queensland: 1 female, Biggenden, May 1973 (ANIC); 1 female, Biggenden, Mar. 1981 (ANIC); 1 female, Brisbane, Sept. 1912 (QM); 1 female, Bluff Range, Apr. 1975 (ANIC); 1 female, Bundaberg, Aug.-Sept. 1971 (ANIC); 1 female, Coast Range, about 13 km south of Biggenden, Jan. 1910 (ANIC); 1 female, Cordalba State Forest, Oct. 1978 (ANIC); 1 female, Eidsvold, Dec. 1922 (AM); 1 female, Hastings Creek, Dec. 1976 (ANIC); 1 female, Hogback Range about 44 mi (= 71 km) west-south-west of Bundaberg, July 1972 (ANIC); 1 female, Iron Range, June 1971 (ANIC); 2 females, Kuranda, Nov. 1952 (AM); 4 females, Mackay, ? 1909 (BMNH); 1 female, Mount Glorius, Dec. 1965 (BMNH); 1 female, Nanango District, Nov. 1927 (QM); 1 female, Yeppoon, Oct. 1924 (AM).

**Description.** *Female.* Length of body 8-12 mm, of forewing 8.9-12.5 mm and of ovipositor (part exserted beyond apex of metasoma) 5.5-7.0 mm. Antennae with approximately 50 flagellomeres. First flagellomere 1.1 and 1.2 times longer than the second and third respectively, the latter being 1.35 times longer than wide. Inter-tentorial distance : tentorio-ocular distance = 1.3:1.0. Face with a well-developed transverse protrusion. Dorsal side of protrusion with a midlongitudinal carina. Facial ratio = 1.36:2.5:1.0. Frons with moderately long setae narrowly near eye, glabrous elsewhere. Ocellar ratio = 1.39-1.56:1.0:4.0-4.3. Head index = 0.82. Mesosoma 3.45-3.78 times longer than high. Pronotum very weakly concave medioanteriorly; moderately setose posterodorsally. Scutellar sulcus finely punctate. Scutellum usually more or less flat in profile. Propodeum usually with strigate to rugose sculpture medially or medioposteriorly. Radial sector ratio = 9.1:6.7:1.0. Submarginal cell ratio = 1.13:2.7:1.0. Hind wing vein ratio = 1.0:2.0. Fore leg ratio = 1.0:1.1:1.9. Fore basitarsal ratio = 8.0. Hind leg ratio = 1.44:2.31:1.0. Hind basitarsal ratio = 6.4. First metasomal tergite approximately 1.2 times wider posteriorly than long; lateral areas wide, largely smooth; median area finely longitudinally striate. Second tergite approximately 2.85 times wider than long, with large smooth anteriolateral areas, elsewhere largely longitudinally striate. Fourth tergite largely longitudinally striate. Fifth tergite with striate to striate-rugose sculpture at least anteriorly. Sixth and subsequent tergites smooth. Ovipositor approximately 0.6 times forewing length. Brownish orange except for the antennae, head, mid-telotarsus, hind tarsus and ovipositor sheaths which are black. Wings grey brown to brown except for the basal third which is dull yellow, and a small area below the pterostigma which is clear to hyaline. Pterostigma largely bright yellow.

**Notes.** Entirely Australian, this species is easily distinguished from related species occurring in Papua New Guinea by its entirely black head. Within Australia this species has been collected mainly in Queensland with just a single specimen each seen by the author from New South Wales and the Northern Territory.

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# Revision of *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 (Gastropoda: Prosobranchia: Eulimidae), Two Genera Parasitic on Sand Dollars

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ABSTRACT. Nine new eulimid gastropods belonging to the genera *Hypermastus* Pilsbry, 1899 and *Turveria* Berry, 1956 are described. Fifteen more eulimids, previously mainly classified in *Eulima* Risso, 1826 and without known hosts are transfered to *Hypermastus* based on shell characters. The species with known hosts are parasitic exclusively on clypeasteroid sea urchins (sand dollars) and parasitise the hosts by penetrating the test with their proboscis and ingesting fluid from the vascular system or the gonads of the host. The snails live on their hosts for periods of a few days and dwell in the sediment most of the time.

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Gastropods of the family Eulimidae are well known to be parasites of echinoderms and numerous species are known to parasitise and to a varying degree be host specific on all kinds of echinoderms (Warén, 1984). Most species are fairly normal looking prosobranchs, but some have become so adapted to their parasitic life that they can only be recognised as molluscs from the veliger larva.

The species discussed here belong to the former group and retain most of the organs present in Caenogastropoda, except a radula.

Classification of eulimids is difficult since the shell is very featureless and many of the most conspicuous features of the shell (e.g. a mucronate larval shell and inflated, thin-shelled whorls) are the result of adaptations to a parasitic life which have evolved independently many times. The mucronate larval shell, for example, is the result of good protection on the host for newly settled snails. This allows rapid growth up to a certain size, when the protection becomes less efficient. Then the snail instead has to produce a shell that can resist attacks by shell cracking predators. When the protection by the host lasts the whole life of the snail (e.g. when the parasite lives in galls or protected among spines) the globular, thin-walled shell morphology is kept also by adult specimens (Warén, in preparation).

The shape of the aperture (not the size) has, however, proved to be a fairly reliable character for generic classification, but is very difficult to describe.

Examination of several hundred species with known hosts (mostly unpublished) has shown that species with similar apertures live on related host echinoderms. It has also become evident that most members of a group of species with similar host choice and morphology of the aperture show other similarities (e.g. fine structure of the proboscis or micro-sculpture of the shell). As a working hypothesis, Warén (1984) has therefore used host choice and shape of aperture for classification, since in most cases preserved material has not been available for detailed anatomical work.

Three of the species discussed in this paper, *Hypermastus placentae*, *H. tenuissimae* and *H. auritae* have been serially sectioned. The anatomy of the proboscis was found to be identical, but this will be discussed in another paper.

Many groups of eulimids are known to parasitise sea urchins and were reviewed by Warén (1984). However, the vast majority of these parasites are associated with species of the Regularia. Only very few species have been reported from the Irregularia.

Habe (1976) described *Curveulima echinocardiaphila* (Japan, parasitic on *Spatangus purpureus* (Pennant)) and *Balcis clypeastericola* (Japan, on *Clypeaster japonicus* Döderlein, 1885). Based on shell morphology, these two species cannot be included in *Hypermastus* or *Turveria*.

There is also one case of a spatangoid sea urchin from the Early Cretaceous (Kiaer, 1981) which had been

parasitised by a supposed eulimid gastropod. The test had been penetrated in a way similar to that described here for *Hypermastus*, and in one case the echinoid had partly repaired the damage, indicating that it was probably not caused by a predator. If this case is correctly assigned to the Eulimidae, it is somewhat surprising since the earliest snails known with certainty to be eulimids are of Late Cretaceous age (e.g. Sohl, 1964).

A few records of eulimids on sand dollars are also found in the echinoderm literature. Guille *et al.* (1986:44) figured *Clypeaster oshimensis* Ikeda, 1935 from New Caledonia, with a eulimid attached on the aboral side. In his large monograph of the sea urchins, Th. Mortensen has some notes on damage of the tests of different species of clypeasteroid sea urchins of the group Laganina, to which suborder the sand dollars belong. He reported (1948:107) that two specimens of *Clypeaster ochrus* H.L. Clark, 1914 were corroded on the aboral side and the spines of this area had regenerated in one of the specimens. Furthermore, (Th. Mortensen, 1948: 262), specimens of *Peronella peroni* L. Agassiz, 1841 were reported to have been drilled by gastropods, but since they were empty tests, it may have been done by a predatory snail. Finally (Th. Mortensen, 1948: 279), specimens of *Peronella japonica* (Mortensen, 1948) collected from 50 m depth, off Misaki Biological Station (Japan) had holes in the test with a tube protruding. The tube is almost certainly a torn-off proboscis of a eulimid.

## Material and Methods

The material on which this paper is based has been accumulated over about ten years of searching museum collections, and more importantly, through collaboration with people who have encountered cases of parasitism and recognised the interest of their findings. The final impetus to produce this paper was Crossland and his collaborators' study of *Hypermastus placentae* (in press) and its biology, which enabled interpretation of observations on other species.

When determining species of Eulimidae, the seemingly featureless shells require that every detail be taken into consideration. This includes a careful examination of the surface structure to find any micro-'sculpture'. This 'sculpture' is often very indistinct and can be seen only in certain illumination. Often it is a refractive phenomenon caused by the structure of the most superficial, partly transparent shell layers and not a real sculpture or unevenness of the surface, visible by SEM. This is the case with all spiral sculpture mentioned in the descriptions. The easiest way to find it is to place the shell at an angle at which the incident light is reflected off the shell, and examine the spots where the light is reflected. By small changes in the angle of the shell in relation to the light, critical areas of the shell, for example the subsutural zone, can be examined. The microsculpture is not visible in the figures, except the subsutural riblets, which are shown in Figure 13B and incremental lines, which can be seen on most specimens of Figure 13.

Eulimids have a strongly periodical growth. Usually they grow 0.5 to 1.5 whorls during a very short period of time. The number of whorls added during each such period is to some extent species specific and varies with the size and the sex. This means that a detailed histogram will show several peaks, corresponding to the different number of growth periods the specimens have passed through. For example, an average adult female *Hypermastus placentae* has about 8.7 teleoconch whorls and is 6.3 mm high, not 6.8 mm as said in Table 3. Actually there are almost no specimens 6.8-7.4 mm high, since this size corresponds to a considerable disturbance of the normal growth pattern. Because of this complicated size distribution, there is little use of measuring a few specimens of a eulimid with periodical growth. The height of a single specimen, combined with information about the growth pattern from the incremental scars is more useful. However, if numerous specimens are available it is useful to measure them for sex and size distribution.

The different proportions of the shells, for example shell height/shell breadth, shell height/aperture height, aperture height/aperture breadth, etc., are extremely constant in the species discussed in this paper and the variation is usually less than ±2% in specimens of the same sex. There are, however, some species, where they are quite variable; perhaps the selective pressure on this character is smaller. Despite that only very few specimens have been examined of *Hypermastus colmani* this is quite obvious. Such case are pointed out in the text.

Because of this small variation it is very important that all figures are prepared with the shells in standardised positions. All photos have therefore been taken with the film plane exactly parallel to the columellar axis of the shells, and all proportions of interest can be obtained from the figures.

Because of a pronounced sexual dimorphism, we have tried to base the descriptions on the females, which are larger and usually easier to determine specifically. In some cases this has not been possible since too few specimens were available to allow recognition of the sexes on a statistical basis. This is pointed out in the descriptions.

Specimens designated as paratypes have as far as possible been selected from the same locality, date and host species as the holotype in order to reduce the risk of mixed lots.

Author names are to be quoted as in the headings of the species.

The location of the material studied is listed under each species, and the reference to collections is made with an abbreviation: AMINZ – Auckland Museum and Institute, New Zealand; AMS – Australian Museum, Sydney; ANSP – Academy of Natural Sciences, Philadelphia; BMNH – British Museum (Nat. Hist.), London; LACM – Los Angeles County Museum of

Natural History, Los Angeles, Ca.; MNHN – Museum National d'Histoire Naturelle, Paris; NM – Natal Museum; NMNZ – National Museum of New Zealand; NMV – National Museum of Victoria; NMW – National Museum of Wales; SAM – South Australian Museum; SBMNH – Santa Barbara Museum of Natural History; SMF – Senchenbergisches Museum und Forschungsinstitut; SMNH – Swedish Museum of Natural History, Stockholm; USNM – U.S. National Museum of Natural History, Washington D.C.; ZMA – Zoological Museum Amsterdam; ZMC – Zoological Museum of Copenhagen; ZMHU – Zoologisches Museum der Humboldtuniversität, Berlin.

Tables referred to throughout the text are in Appendix 1.

## Biology

Here some observations and conclusions about the biology are summarised. They refer almost exclusively to species of *Hypermastus* since virtually nothing is known about those classified in *Turveria*, except that they are found on species of the sand dollar genus *Encope*.

**Host specificity.** In this paper, nine new species of *Hypermastus* are described, bringing the number of species with known hosts up to twelve. Three of these are described from undetermined 'sand dollars', two are known from *Peronella leseuri*, three are known exclusively from *Echinodiscus bisperforatus*, and two from both *E. bisperforatus* and *E. auritus*. The apparently high number from *E. bisperforatus* may be surprising considering that there are about 122 known species of the order Clypeasterida (Mortensen, 1948), but the explanation for this may be that *E. bisperforatus* is a very common species, and the material available originates from a few intertidal localities with *Echinodiscus bisperforatus* occurring at least four of these (possibly more since some hosts were not determined). The two species of *Turveria* have both been found on two species of *Encope* which occur sympatrically.

From this sparse material it is difficult to draw any conclusions about the host specificity of the species of *Hypermastus*, but it seems that they follow the same pattern as in other species of Eulimidae with most species occurring on a few related hosts with similar biology. Often the main occurrence is on a single host species with rarer occurrences on the other host species (Warén, 1984).

**Infestation rates and life on host.** Nothing is known about the infestation rates for most of the species since most of the material is 'second hand'. At one occasion there were specimens of *H. auritae* on every fourth host. Nine specimens of *H. sauliae* were obtained from 45 hosts. Crossland *et al.* (in press) found the rate for *H. placentae* to vary, at the same site, from 25% to close to zero between April 1988 and March 1989. Two possible explanations of this variation were suggested: recruitment and seasonal variation in time spent on the host.

Large specimens of *H. placentae* spend a longer time on the host than do small ones. Ten females (height range 6.12-8.14 mm, mean 7.46 mm) spent an average 8.9 days on the host, during an 18 day period. Eight smaller specimens (height range 3.64-6.96 mm, mean 4.69 mm) spent on an average 2.2 days attached during the same period. It is possible that they were males with empty gonads, after having mated several times.

**Feeding biology.** No species of *Hypermastus* have a radula and feeding must therefore take place by ingesting coelomic fluid, or by (less likely) dissolving gonadal tissues and ingesting the resulting fluid. Of 19 specimens of *H. placentae* examined, six were found with the proboscis ending in gonadal tissues, 13 with the proboscis ending in the coelomic cavity (Crossland *et al.*, in press). The high frequency of parasitism on the gonads may be due to the body fluids there being richer in nutrients.

**Penetration of the host.** When species of *Hypermastus* parasitise their hosts, they make a hole in the porous skeleton which constitutes the test. Such penetrations made by *H. boschorum*, *H. placentae* and *H. tenuissimus* have been examined and are described in more detail below. It is rare to find these holes in the process of healing, suggesting that they are repaired by the host in a short time compared with the time that the parasites spend on the host. The time spent on the host is, in the case of females of *Hypermastus placentae*, about nine days (Crossland *et al.*, in press), and the scars must therefore heal in a few days.

The method used for penetrating the skeletal network of the test is not known, but the structure of the skeletal network surrounding the holes (all elements tapering to fine points or rounded, Fig.11) clearly indicates that it has been dissolved. This is probably also the case with the tissues. Where large parasites are found attached to the test, it is denuded of pedicellariae and spines around the hole.

The holes characteristically consist of a large pit, with a fine hole in the bottom. The pit is filled by the pseudopallial collar of the proboscis, which probably aids in the attachment of the parasite to the host, so it is not easily dislodged.

This structure of the sides and the shape of the pit with a much narrower hole for the final penetration of the test, may be of help in recognising the origin of scars in fossil clypeasterids.

**Sexual conditions.** *Hypermastus placentae* is a gonochorist with males of a smaller average size. Crossland *et al.* (in press) found the males of *H. placentae* to have an average length of $4.17 \pm 1.69$ mm, while the females were $6.82 \pm 0.92$ mm. The sex of these specimens had been histologically determined, and no specimens with both testis and ovary were found, which suggests that protandry is not involved. Crossland *et al.* (in

press) occasionally found large males of a shell height corresponding to mature females. This can perhaps be explained by scattered females changing sex to males or more likely that some males continue growing after their reproduction. There is an indication that the same happens in *H. tenuissimae*, where a large, sectioned specimen proved to be a male, but it has not been encountered in other, typically gonochoristic eulimid genera like *Melanella* and *Vitreolina* where hundreds of specimens have been sexed by external sexual characters and/or histology of the gonads (Warén, unpublished).

An attempt to determine the sex from shell morphology based on the paratypes of *Hypermastus placentae* gave very similar results regarding the height of the sexes and the height distribution (see Table 3). It can therefore be assumed that similar attempts on *H. boschorum* and *H. auritae* based on shell morphology only, are reliable.

The bimodality of the size frequencies of several other species fits with this and also with the fact that most species of the Eulimidae have a strong sexual dimorphism, with males smaller than two thirds of the height of the females.

Measurements of 26 *Turveria encopendema* and 23 *T. schwengelae* did not reveal any noticeable bimodality in the height frequency, and therefore it is unlikely that they have a distinct sexual dimorphism. However, this needs confirmation by examination of the soft parts. (The two species may be protandrous or simultaneous hermaphrodites, which is common among eulimids, while equal height of the sexes is unknown in the family.)

**Spawning and larval development.** *Hypermastus placentae* spawns in August–September, perhaps also later (Crossland *et al.*, in press). No egg capsules have been found on the hosts, so it seems likely that these are deposited in the sand where the sea urchins live. It is usually difficult to interpret the mode of larval development from larval shells of eulimids, because protoconch 1 is not very clearly demarcated in species known to have planktotrophic development. This is true also for species of *Hypermastus*, but it seems very likely that most of the species, have planktotrophic larvae.

## *Hypermastus* Pilsbry, 1899

**Type species.** *Hypermastus coxi* Pilsbry, 1899 by original designation (Fig.4A-B).

**Description.** Eulimids parasitic on sand dollars, with a small to large (3-30 mm), colourless, cylindrical or slender and conical shell with slowly increasing diameter of the flat or very slightly convex whorls. Aperture rather small with the line columella-parietal wall almost straight, slightly arched or with a very weak angle at the transition from columella to parietal wall. Profile of outer lip straight or curved with the median part protruding. Proboscis fully retractile and equipped with a small pseudopallial collar.

**Remarks.** The genus *Hypermastus* was described by Pilsbry (1899) for a new species of Eulimidae known from shells from New South Wales (Australia). Since then specimens with soft parts have been found at several localities in New South Wales (unpublished material in the Australian Museum), but no specimens have been found associated with their host and we have seen no specimens with preserved soft parts good enough to be examined anatomically.

Warén (1980) used this genus for two new species which were described from Borneo (*H. sauliae* and *H. echinodisci*). They had been found on the sand dollar *Echinodiscus bisperforatus* (Leske, 1778) (Echinoidea, Irregularia, Clypeasteroidea, Scutellidae). The assignment of these two species to *Hypermastus* was based on shell characters only, and the present use of this generic name is still not more firmly founded.

Nevertheless, additional species found later have not disturbed this, but rather have formed a more continuous series, from species similar to *H. coxi* with a cylindrical shell and strongly set off larval shell, via those with an evenly conical spire, to those with a slightly irregular shell and almost *Lymnaea*-like (Pulmonata) aperture. All these species have been found on sea urchins of the order Clypeasterida; no species known from other echinoderms closely resemble *Hypermastus*.

The two genera treated in this paper, *Turveria* and *Hypermastus*, are quite similar in shell morphology but as no specimens of *Turveria* have been available for anatomical examination, we have preferred to keep them apart since *Turveria* has a coloured shell. A coloured shell is uncommon in the Eulimidae and is mostly restricted to the most unmodified taxa, such as *Eulima* Risso, 1826, *Niso* Risso, 1826, and *Hemiliostraca* Pilsbry, 1918. It can therefore not be excluded that *Turveria* is an earlier branch from an ancestral stock of coloured species. There is also a difference in the microsculpture. *Turveria* has a dense coating of sharp and uniform incremental lines, while in *Hypermastus* there are occasional, scattered, irregular and indistinct lines only, which by no means cover the surface as in *Turveria* (Fig.13A,B).

We have in this paper also included a number of eulimids known only from the shell, but from shell morphology they can be placed together with those of which we know the host.

### *Hypermastus acutus* (Sowerby, 1834)

Fig.1A,B

*Eulima acuta* Sowerby, 1834: 8.

**Type material.** HOLOTYPE (Fig.1A,B) BMNH 1967989.

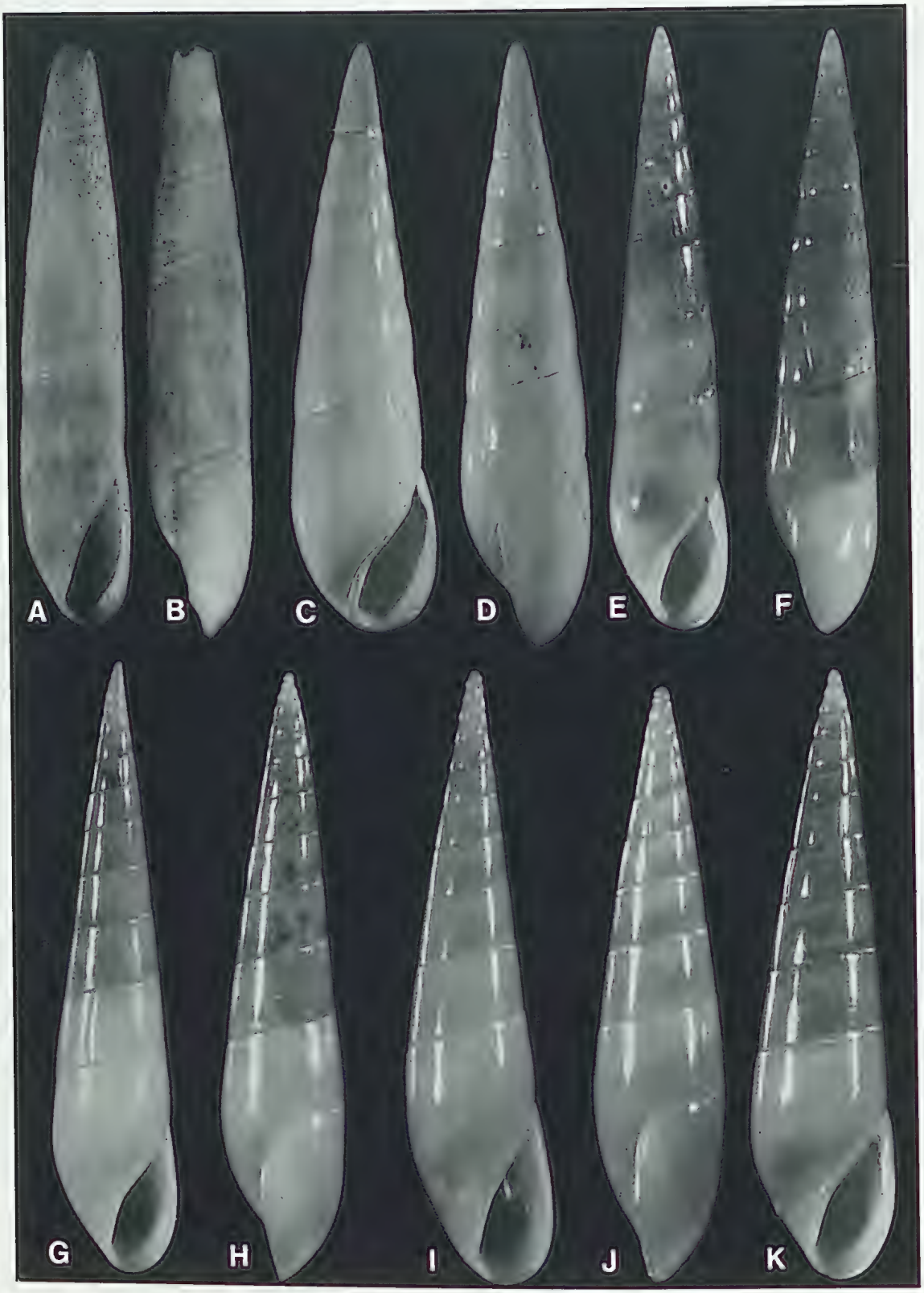


**Fig.1.** A–B. *Hypermastus acuta* (Sowerby, 1834), holotype, BMNH 1967.989, 7.9 mm. C–F. *H. acuta* (A. Adams, 1851), syntypes. C–D. BMNH 1962.289, 23.7 mm. E–F. BMNH 1962.289, 17.4 mm. G–K. *H. auritae*. G. holotype, female, 12.2 mm. H. paratype, female, SMNH 4114, 11.1 mm. I. paratype, male, SMNH 4114, 7.50 mm. J. paratype, male, SMNH 4114, 7.25 mm. K. female, from *Echinodiscus bisperforatus*, SMNH, 7.96 mm.

**Type locality.** Bay of Montijo, Pacific side of Panama, 24 m. Host species unknown.

**Material examined.** The holotype.

**Distribution.** No reliable additional records exist.

**Remarks.** The holotype (Fig.1A,B) is in poor condition, corroded and without apex. The aperture is very similar to the most slender species of *Hypermastus*, and we provisionally place it here.

### *Hypermastus acutus* (A. Adams, 1851)

Fig.1C–F

*Eulima acuta* A. Adams, 1851: 276 (not Sowerby, 1834).

**Type material.** Two SYNTYPES (Fig.1C-F) BMNH 1968269.

**Type locality.** Philippines, Luzon, "prov. Cangisanan, Sual", 13 m. Host species unknown.

**Material examined.** The type material.

**Distribution.** No reliable additional records exist.

**Remarks.** This is a large species of *Hypermastus*, one of the syntypes measuring 23.8 mm. It resembles *H. producta* and *H. epepterion*, but differs from them by having a much more rapidly increasing diameter of the apical whorls. In some species, however, this is subject to variation within a species (see *H. auritae*), and richer material will be needed to solve the problem with the relations between the specimens on which these names are based.

*Hypermastus acuta* A. Adams also resembles the holothurian parasite *Melanella teinostoma* (A. Adams, 1851) in the general shape of the shell, but that species has a sinuated, opisthocline outer lip.

*Hypermastus acuta* A. Adams is a homonym of *H. acuta* Sowerby, but the species of Eulimidae are poorly known presently and there may very well exist another name for A. Adams' species. We have therefore preferred not to suggest a replacement name until the problems above are solved.

### *Hypermastus auritae* n.sp. Warén

Figs 1G–K, 13I

**Type material.** HOLOTYPE (SMNH 4114, Fig.1G) and 45 PARATYPES; SMNH 4115, AMS C160819, BMNH 1989153, USNM 860502 and coll. D. Bosch, all from type locality.

**Type locality.** Oman, Masirah Island, just above low tide, 22 Dec. 1988, in fine clean sand, on *Echinodiscus auritus* (Leske, 1778). About every fourth host infested.

**Material examined.** The types and Quram Beach, near Muscat, water edge at extreme low tide, muddy sand, on *Echinodiscus bisperforatus* (Leske, 1778), leg. D.T. Bosch, 6 Nov. 1987, 1 specimen, SMNH.

Same locality and host, Mar. 1987, leg. D.T. Bosch, 1 female, SMNH.

**Description.** Shell (Fig.1G-H) tall, slender, conical, fairly solid, semitransparent, with crenulated suture and small aperture. Larval shell (Fig.13I) distinctly set off, sometimes mucronate, consisting of about 1.5 distinctly convex whorls; height 0.24-0.32 mm depending on how much is concealed by the subsequent whorl. Teleoconch of holotype has 12.6, very flat, almost perfectly smooth and polished whorls. Unsculptured except for some very short but rather conspicuous and regularly spaced incremental lines just below suture, giving the uppermost part of the whorls a crenulated appearance (similar to *H. kilburni*, see Fig. 13B). These lines are situated about 0.03-0.05 mm apart on top whorls, 0.15 mm apart on body whorl. Holotype with about 8 incremental scars, 1.3, 2.0, 4.0, 5.3, 6.6, 9.0, 10.0, and 11.5 whorls from outer lip, but their number and position subject to a good deal of individual variation. Height of subsutural zone 20% of height of whorls. Aperture small, with parietal wall and columella forming distinct angle. Outer lip distinctly retracted at suture, evenly curved, and approximately orthocline.

**Dimensions.** Height of holotype 12.2 mm.

**Male** (Fig.1I-J). About two thirds the height of the female and has more narrow aperture with less distinct angle between parietal wall and columella.

**Remarks.** The diameter of the apical whorls is quite variable since in one female they are rapidly increasing their diameter, almost like in *H. coxi*, while in the other specimens they are very slender.

Forty one specimens of the type sample were measured and Table 1 shows the height and sex distribution.

*Hypermastus auritae* closely resembles *H. kilburni* from Mozambique, but that species has more convex whorls and more conspicuous and distant growth lines below the suture.

The smallest females examined, both from *E. bisperforatus*, are 6.1 and 7.9 mm high and are thus smaller than, or of the same height as the largest males. Nevertheless they can easily be recognised as females from the broader shape of the aperture (compare Fig. 1I and 1K).

### *Hypermastus boschorum* n.sp., Warén

Figs 2A–C, 11E, 13J

**Type material.** HOLOTYPE (SMNH 4116, Fig.2A) and 20 PARATYPES; SMNH 4117, AMS C160816, BMNH 1989152, USNM 860500, and coll. D. Bosch, all from type locality.

**Type locality.** Muscat, Quram Beach, extreme low tide, muddy sand, 6 Nov. 1987, leg. D.T. Bosch, all on *Echinodiscus bisperforatus*.

**Material examined.** The types and Muscat, 0.6 m depth, on *Echinodiscus bisperforatus*, Mar. 1987, leg. D.T. Bosch, 4 specimens, SMNH. Muscat, Quram Beach, extreme low tide, muddy sand, on *Echinodiscus bisperforatus*, Nov. 1988, leg. D.T. Bosch, 3 specimens, SMNH. Muscat, Quram Beach, on a young *Echinodiscus auritus* (46 mm diameter), Nov. 1988, leg. D.T. Bosch, 1 specimen, SMNH.

**Description.** Shell (Fig.2A,B) straight, slender, glossy, transparent with small, indistinctly off set larval shell and constricted aperture. Larval shell (Fig.13J) 0.35 mm high and consisting of almost 2 slightly convex whorls. Holotype with 9 1/4 almost flat teleoconch whorls sculptured by 50-80 barely visible (at 50x) spiral lines of rows of granules (not visible by SEM) and by close set, indistinct incremental lines. Adult specimens have about 10 irregularly disposed, straight, not very strong incremental scars. Suture shallow, indistinct, well visible only at incremental scars and in reflected light. False suture distinct. Width of subsutural zone corresponding to one third of height of whorls. Aperture small and narrow, its upper part constricted by deflected outer lip.

**Dimensions.** See Table 2. Height of holotype 5.93mm.

**Male** (Fig.2C). Three quarters the height of female and more slender. No difference in shape of aperture.

**Remarks.** *Hypermastus boschorum* resembles *H. sauliae*, but that species is smaller (3.5-5.5 mm high) and has about half a whorl more in the larval shell. The diameter of the protoconch of *H. sauliae* is smaller and its shape is more conical (see Fig.13K). The maximum diameter of the shell corresponds to 23% of the height in *H. sauliae* while *H. boschorum* is slightly broader at 25%.

The specimens were found attached to the host both ventrally and dorsally, and remained attached when the host was shaken in sea water.

Cleaning the test of one parasitised host revealed several perforations (Fig.11E).

The height of 27 specimens was measured and two distinct size classes, presumably males and females, were found (Table 2).

### *Hypermastus bulbula* (Murdoch & Suter, 1906)

Fig.2D–G

*Eulima bulbula* Murdoch & Suter, 1906: 297.
*Balcis pervegrandis* Powell, 1940: 233.
*Balcis* (*Hypermastus*) *bulbula*.–Powell 1979: 141.

**Type material.** *Eulima bulbula*, HOLOTYPE (Fig.2F,G), NMNZ M 1774; *B. pervegrandis*, in AMINZ, not available. Host species unknown.

**Type localities.** *Eulima bulbula*, off Great Barrier Island, New Zealand, 200 m; *B. pervegrandis*, off Ahipara, New Zealand, 44 m.

**Material examined.** The holotype of *E. bulbula* and New Zealand, north of the Cook Strait, 40°33.5'S 174°59.5'E, 86-88 m, 2 specimens, NMNZ M 52710.

**Distribution.** Only known from New Zealand.

**Remarks.** On shell characters *Hypermastus bulbula* is most appropriately classified in the genus *Hypermastus*.

We have not been able to examine the type of *B. pervegrandis*, but follow Powell's synonymisation (1979).

There are several possible host urchins in New Zealand. Most likely is perhaps *Peronella hinemoae* Mortensen, 1921.

### *Hypermastus casta* (A. Adams, 1861)

Figs 2H–J, 3A–D

*Leiostraca casta* A. Adams, 1861: 240.
*Leiostraca constantia* A. Adams, 1861: 240.
*Leiostraca maria* A. Adams, 1861: 240.

**Type material.** *Leiostraca casta*, SYNTYPE (Fig.2H,I) NMV 31376; *L. constantia*, SYNTYPE (Fig.2J) NMV 31352, is the young of *L. casta*; *L. maria*, SYNTYPES (Fig.3A-D) NMV 31373. This is also the young of *L. casta*.

**Type locality.** *Leiostraca casta*, Shan-tung (Hwan) and Lian-tung (Hulu-shan Bay), 5.5 m; *L. constantia*, Lian-tung (Hulu-shan Bay), 5.5 m, sand and shells; *L. maria*, Gulf of Pe-chili, 5.5 m, mud (all localities in northern China). Host species unknown.

**Material examined.** The types listed above.

**Distribution.** No reliable additional records exist.

**Remarks.** This species has not been recorded since the original description, and we have not seen any further specimens that safely can be assigned to it. We have not figured any larval shell of this species since it

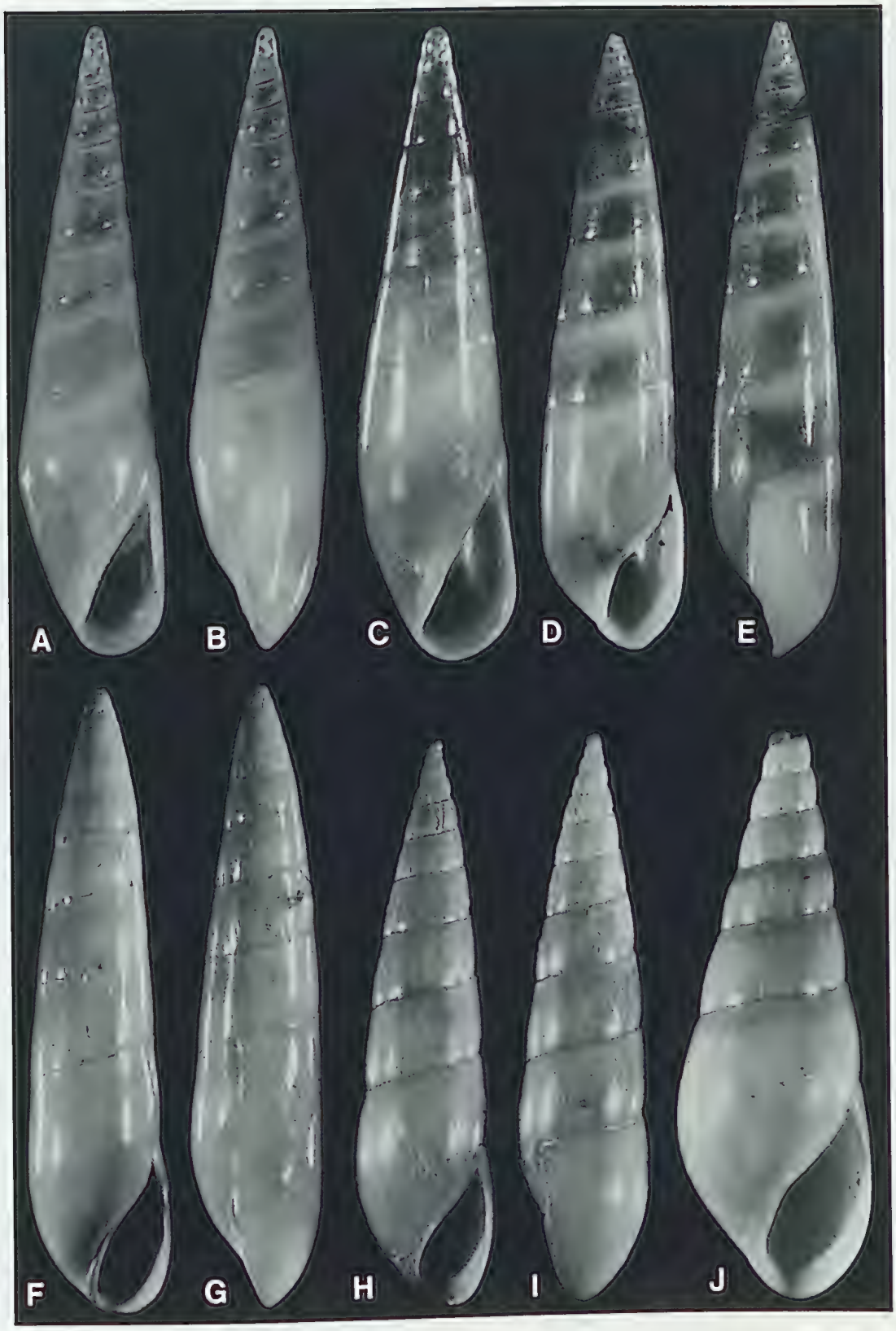


**Fig.2.** A–C. *Hypermastus boschorum*. A. holotype, 5.93 mm. B. paratype, female, SMNH 4117, 6.26 mm. C. paratype, male, SMNH 4117, 4.29 mm. D–G. *H. bulbula*. D–E. New Zealand, 40°33.5'N 174°59.5'E, 86-88 m, NMNZ M 52710, 11.6 mm. F–G. holotype, NMNZ M 1774, 12.4 mm. H–I. *H. casta*, syntypes, NMV F 31376. 9.88 mm. J. *Eulima constantia*, syntype, NMV F 31352. 5.6 mm.

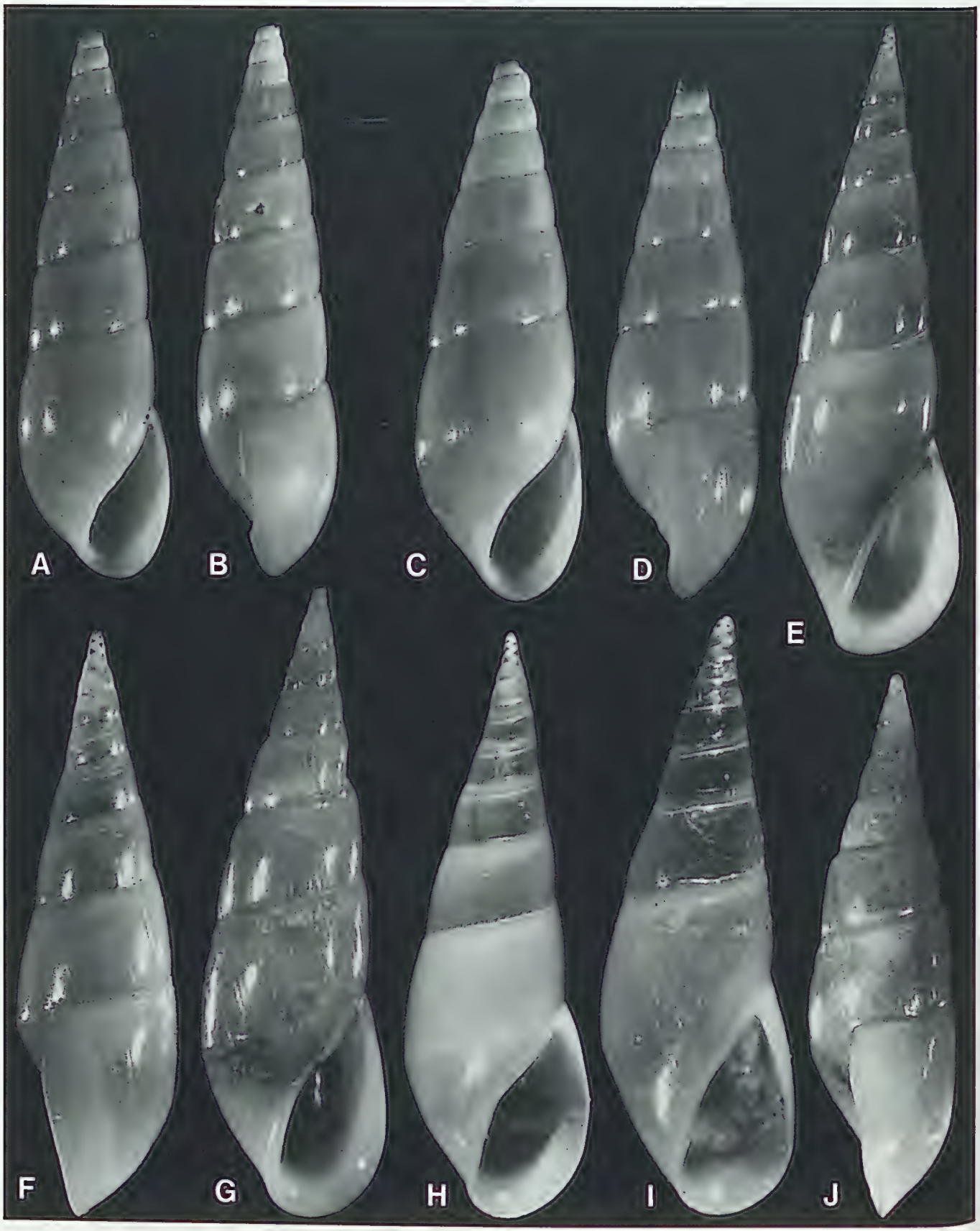


**Fig.3.** A–D. *Eulima maria*, syntypes, NMV F 31373, A–B 6.81 and C–D 9.96 mm. E–F. *Hypermastus colmani*, holotype, AMS C69735. 8.4 mm. G–J. *H. colmani*. G. J. paratype, female, AMS C160814, 8.0 mm. H. female, SMNH 4118, from AMS C117597, 7.3 mm. I. male, SMNH 4118, from AMS C117597, 3.60 mm.

was broken in all syntypes. It should be possible to recognise *L. casta* from the distinctly convex whorls and rounded aperture.

The presence of this type material in the National Museum of Victoria is somewhat surprising, but Warén has seen no types in other collections. A list of possible types of species described by A. Adams and present in that collection was published by Boyd & Phillips (1985).

### *Hypermastus colmani* n.sp., Warén

Figs 3E–J, 12J

**Type material.** HOLOTYPE (AMS C69735, Fig.3E,F), 1 PARATYPE, now AMS C160814 (both from AMS C69735) and 2 PARATYPES SMNH 4118 (from AMS C117597).

**Type locality.** "On large red sand dollar", (presumably *Peronella leseuri* [Valenciennes, 1841]), Urangan, Queensland (AMS C69735).

**Material examined.** The type material and Dingo Beach, south of Bowen, Northern Queensland, "on oral surface of flat biscuit urchin" (presumably *Peronella leseuri*), leg. P.H. Colman, 30 May 1977, 1 female, broken, 1 female 7.12 mm, 1 male 5.12 mm sectioned, 1 female 7.3 mm, 1 male 3.6 mm, AMS C117597.

**Description.** Shell (Fig.3E-J) high, straight, conical, transparent and glossy with convex whorls and large expanded aperture. Larval shell (Fig.12J) consisting of about 3 distinctly convex whorls, height 0.46 mm. Holotype has 7.5 unusually convex whorls, which are almost perfectly smooth, sculptured only by some weak and irregular traces of incremental and spiral lines. Incremental scars situated 3.3, 2.1 and 1.0 whorls from larval shell; rather strong and straight. Suture distinct. False suture distinct on the apical whorls, hardly visible on lower ones. Aperture large and expanded. Outer lip evenly curved, straight and prosocline.

**Dimensions.** Height of holotype 8.4 mm.

**Male** (Fig.3I). Height about two thirds of height of female and shell of more slender shape and with less distinct angle between parietal wall and columella.

**Remarks.** *Hypermastus colmani* is characterised by the fairly large and conical shell with unusually convex whorls and the large, expanded aperture. It resembles *H. echinodisci*, but the shell of that species is smaller (about 5 mm high), has a rougher surface, and a larval shell of about two whorls, (height 0.38 mm). *Hypermastus obliquistomum* differs in having a more cylindrical shell with a smaller larval shell of about 2.5 whorls and a height of 0.42 mm.

### *Hypermastus coxi* (Pilsbry, 1900)

Figs 4A–D, 13D

*Eulima* (*Hypermastus*) *coxi* Pilsbry, 1899: 258.
*Hypermastus mucronata*.–Laseron 1955: 86 (not Sowerby, 1866).

**Type material.** HOLOTYPE (Fig.4A,B) ANSP 71306. Host species unknown.

**Type locality.** Port Stephens, NSW, Australia.

**Material examined.** The holotype and Twofold Bay, NSW, 27-128 m, 1 specimen, AMS C120739; Twofold Bay, NSW, 9 m, 1 specimen, AMS C66118.

**Remarks.** This species is so far only known from shells, with dried, rotten soft parts. It resembles a miniature of *H. mucronata*, and from the beginning we were inclined to consider it a dwarf male of that species, but since the larval shells are different this is most unlikely. We have never seen rich material with both species present.

*Hypermastus coxi* can be recognised from the small, cylindrical shell and the mamillate larval shell of slightly more than 1.5 whorls and a height of about 0.20 mm. The position of the larval shell in relation to the following sutures is very variable, as often is the case in eulimids with small mamillate protoconchs and rapid post larval growth. This makes the measurements uncertain.

### *Hypermastus cylindrica* (Sowerby, 1900)

Figs 4E,F, 12E

*Mucronalia cylindrica* Sowerby, 1900: 127.

**Type material.** HOLOTYPE (Figs 4E-F,12E) BMNH 1900.11.18.40.

**Type locality.** Cebu, Philippines. Host species unknown.

**Material examined.** The type material.

**Distribution.** No reliable additional records exist.

**Remarks.** No additional specimens are known of this species, but the shape of the aperture and the outer lip make it likely that this species belongs to *Hypermastus*.

### *Hypermastus echinodisci* Warén, 1980

Figs 4G,H, 13C

*Hypermastus echinodisci* Warén, 1980: 291.

**Type material.** HOLOTYPE and several PARATYPES,

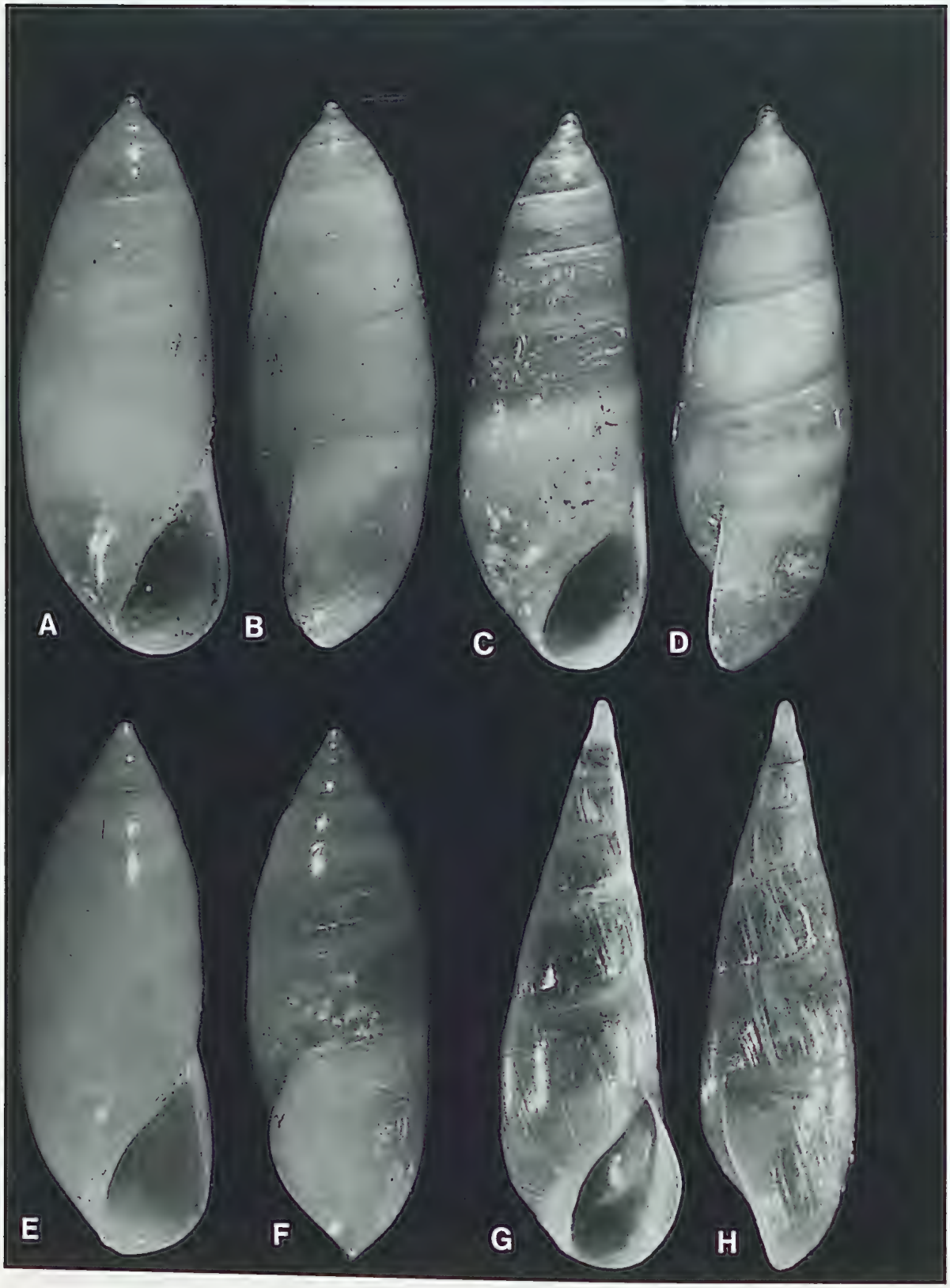


**Fig.4.** A–D. *Hypermastus coxi*. A–B. holotype, ANSP 71306, 4.0 mm. C. Twofold Bay, New South Wales, 27-128 m, AMS C120739, 4.32 mm. D. same locality, 9 m, AMS C66118, 4.16 mm. E–F. *H. cylindrica*, holotype, BMNH 1900.11.10.40, 6.95 mm. G–H. *H. echinodisci*, MNHN ex M. Saul, 4.8 mm.

ANSP 349451 and 349452.

**Type locality.** Tanjong, Aru, Jesselton, Sabah (North Borneo), on *Echinodiscus bisperforatus*.

**Material examined.** The type material and Merang Beach, Trengganu State, Malaysia, 5°32.3'N 102°56.8'E, lowest intertidal zone, "sparse sand dollars heavily infested", leg. T.E. Yancey 13 Aug. 1974, 3 young specimens, USNM 853989; Tanjong, Aru, Jesselton, Sabah (North Borneo), leg. M. Saul, 1 specimen, MNHN.

**Distribution.** Only known from the material examined, from Malaysia and Borneo, intertidal.

**Remarks.** *Hypermastus echinodisci* may be recognised by the expanded, *Lymnaea*-resembling aperture, which is more irregular than in *H. obliquistomum* and *H. colmani*, both of which are also considerably larger.

### *Hypermastus epeterion* (Melvill, 1889)

Figs5A–B,12I

*Eulima epeterion* Melvill, 1889: 31.

**Type material.** HOLOTYPE (Figs 5A-B, 12I) in NMW.

**Type locality.** Mauritius. Host species unknown.

**Material examined.** The holotype.

**Distribution.** No reliable additional records exist.

**Remarks.** No additional information is available about this species. It is so far known only from the type. It resembles *H. epiphanes*, but that species has flatter apical whorls. It is unusually large for the genus, 16 mm high.

### *Hypermastus epiphanes* (Melvill, 1897)

Fig.5C,D

*Eulima epiphanes* Melvill, 1897: 13.

**Type material.** Several SYNTYPES in NMW, 1 SYNTYPE AMS C40863, 1 SYNTYPE SMNH 4124 (Fig.5C,D), all from type locality.

**Type locality.** Linjah, Persian Gulf, 9 m, soft mud. Host species unknown.

**Material examined.** The type material.

**Distribution.** No reliable additional records exist.

**Remarks.** Very similar to *H. epeterion*, but *H. epiphanes* has flatter apical whorls. Also this is an unusually large species, 14 mm high.

### *Hypermastus georgiregis* (Cotton & Godfrey, 1932)

Figs5E–F,12A

*Eulima georgiregis* Cotton & Godfrey, 1932: 37.

**Type material.** HOLOTYPE (Figs 5E-F,12A) SAM D 10631

**Type locality.** King George Sound, SA, 40-50 m. Host species unknown.

**Material examined.** The type material.

**Distribution.** No reliable additional records exist.

**Remarks.** *Hypermastus georgiregis* is, judging from shell characters, an unquestionable member of this group of sand dollar parasites. The profile of the outer lip and the weak angle between the columella and parietal wall is very similar to all other species with known hosts. Nothing is known about its biology. It resembles *H. mucronata*, but has more convex whorls and a larger larval shell (about 0.23 mm diameter instead of 0.18 mm). However, it cannot be excluded that they are synonyms.

### *Hypermastus indistincta* (Thiele, 1925)

Fig.5G–I

*Eulima indistincta* Thiele, 1925: 309.

**Type material.** HOLOTYPE and 6 PARATYPES (Fig.5G-I) in ZMHB, all no 101928.

**Type locality.** Padang, Sumatra. Host species unknown.

**Material examined.** The type material.

**Distribution.** No reliable additional records exist.

**Remarks.** We have seen only the type material of this species, which resembles *H. tenuissimae* but has a less straight spire and attains a larger height (at least 9 mm). *Hypermastus indistincta* also resembles *H. boschorum*, but that species has a more straight spire and a proportionally larger aperture.

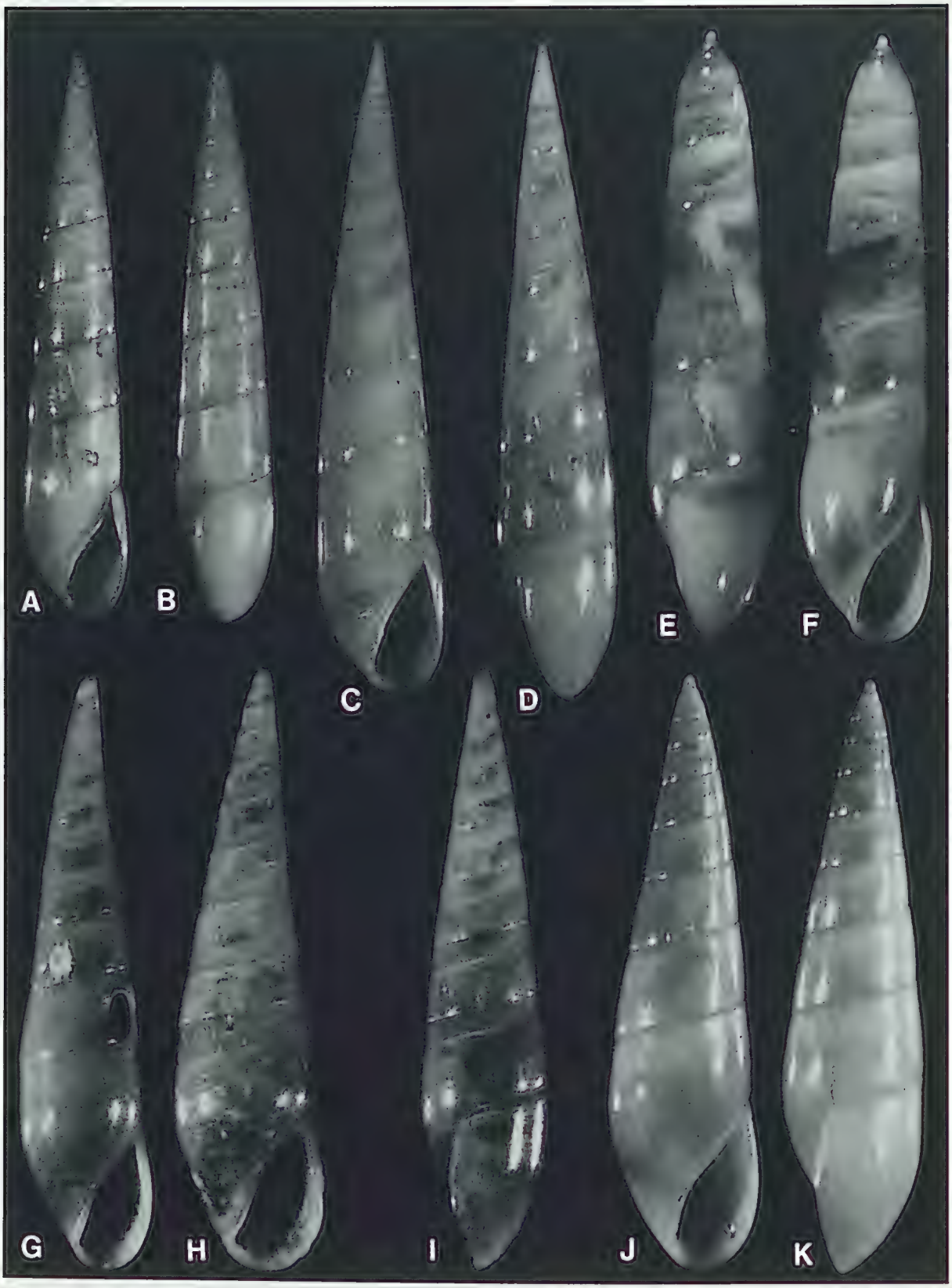


**Fig.5.** A–B. *Hypermastus epeterion*, holotype, 16.1 mm. C–D. *H. epiphanes*, syntype, 13.8 mm, SMNH 4124. E–F. *H. georgiregis*, holotype, SAM D 10631, 12.0 mm. G–I. *H. indistincta*. G. holotype (drilled) 9.3 mm. H–I. paratypes, H. (male?) 4.7 mm and I. 7.9 mm. J–K. *H. kilburni*, holotype, NM G 3676/T70, 9.00 mm.

### *Hypermastus kilburni* n.sp., Warén

Figs5J–K,13B,E

**Type material.** HOLOTYPE (Fig.5J-K) NM G 3676/T69; paratypes, 11 young specimens, NM G 2106/T70, from the same locality, "on sand dollars", and 3 young specimens SMNH 4119, from NM G 2106/T70.

**Type locality.** Mozambique, Bazaruto Island, parasitic on an 'echinoid'.

**Material examined.** The type material.

**Distribution.** No additional records exist.

**Description.** Shell (Fig.5J-K) tall, conical, slightly convex, solid, with mucronate larval shell. Larval shell (Fig.13E) distinctly set off, with about 1.5 perfectly flat whorls and height of about 0.26 mm. Holotype has 9.3 indistinctly convex teleoconch whorls, of which first 2 whorls increase their diameter much faster than subsequent ones. Sculpture consisting of some irregularly scattered incremental lines and 6 incremental scars situated 1.5, 2.7, 3.5, 4.5, 5.4 and 7.4 whorls from outer lip. In addition, there are numerous, regularly appearing short incremental riblets at the suture, about 0.1 mm long and with intervals of 0.1-0.04 mm. Suture distinct. Aperture rather high and slender, slightly excavated in its lower part. Outer lip retracted at suture, slightly and evenly convex and orthocline.

**Dimensions.** Height of holotype 9.05 mm.

**Male.** Not known. Specimen described assumed to be female.

**Remarks.** *Hypermastus kilburni* is based on two lots from the same locality, collected by different collectors. The description is based on the holotype, which comes from a lot of a single adult specimen, the paratypes come from a sample of 14 young specimens (NM G 2106).

*Hypermastus kilburni* resembles *H. auritae*, but has more crowded incremental riblets at the suture, a rougher surface with more distinct growth lines and distinctly convex whorls. It also resembles *H. serratus*, but that species has more distinctly convex whorls and a more strongly convex profile of the outer lip.

### *Hypermastus minor* n.sp., Warén

Figs6A,B,12F

**Type material.** HOLOTYPE (Fig.6A,B) USNM 778727.

**Type locality.** "On juvenile echinoids, *Echinodiscus bisperforatus*, mid-intertidal area of very wide sand beach" (label, presumably T.E. Yancey), Konchung Laut Village, 32 km south of Klang, Selongor State, Malaysia, leg. T.E. Yancey, 10 Mar. 1974, 1 adult specimen, USNM 778727.

**Material examined.** The holotype and Tanjong Aru, Jesselton, Sabah (North Borneo), leg. M.Saul, on *Echinodiscus bisperforatus* (together with numerous *H. sauliae*), 1 specimen, SMNH.

**Distribution.** Only known from the material examined.

**Description** (sex not known). Shell (Fig.6A,B) small, solid, and glossy. Left side evenly convex, right side straight with proportionally large aperture. Larval shell (Fig.12F) consisting of almost 3 slightly convex whorls (height 0.45 mm). Holotype has about 4.7 almost perfectly flat whorls, with very fine and indistinct spiral microsculpture. Suture very shallow but distinct. Teleoconch with 4 straight, not very distinct incremental scars on lower 3 whorls. Aperture large with almost perfectly straight parietal wall, reaching far over to the left side. Outer lip slightly prosocline, indistinctly retracted at suture, slightly and evenly convex below suture.

**Dimensions.** Height of holotype 3.68 mm (larval shell missing).

**Remarks.** Despite being known from only two specimens, and we find this species characteristic enough

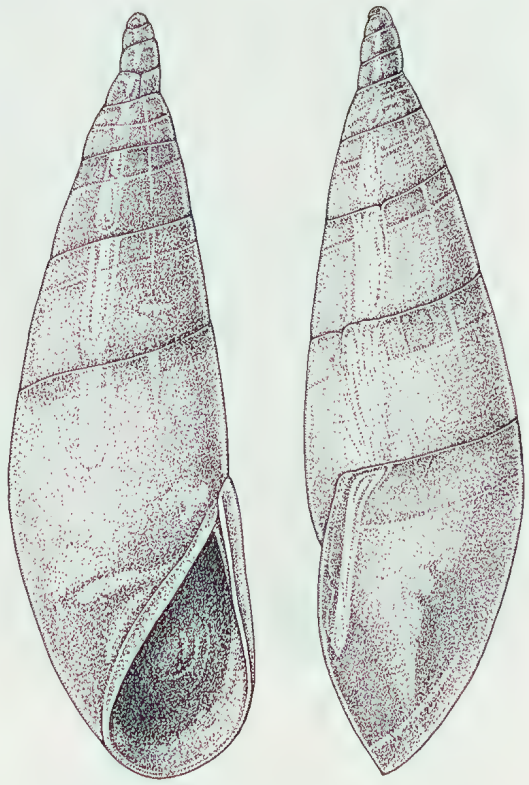

**Fig.6.** *Hypermastus minor*, holotype, 4.0 mm.

to be described. The general shape of the shell with the outer lip and the right side forming a straight line and the left side evenly curved differs from all other species of *Hypermastus*. The aperture on the other hand, especially the straight parietal wall and the shape of the outer lip does not differ from what is normal within the genus.

### *Hypermastus mucronata* (Sowerby, 1866)

Figs7A–D,12E

*Eulima mucronata* Sowerby *in* Reeve, 1866: sp. 42.
*Hypermastus coxi*.–Laseron 1955: 86.

**Type material.** SYNTYPES (Fig.7A,B) BMNH 1870.10.26.114.

**Type locality.** Port Jackson, NSW, from G.F. Angas. Host species unknown.

**Material examined.** The type material and several lots in AMS, from New South Wales and southern Australia.

**Distribution.** New South Wales and southern Australia, shallow water (material in AMS).

**Remarks.** No additional information about this species is known, although the species is not rare. It resembles *H. georgiregis*, *H. philippiana* and *H. colmani*, but has flatter whorls than any of these. From *H. colmani* it differs also by having a more blunt larval shell and a strongly prosocline and straight outer lip.

### *Hypermastus obliquistomum* n.sp., Warén

Figs7E,F,12H

**Type material.** HOLOTYPE AMS C160815, (Fig.7E,F), from AMS C117611.

**Type locality.** "From sand dollars", Baie des Isoles, Noumea, New Caledonia, mudflats, ventral side of host, leg. P.H. Colman, 15 May 1971, together with a single specimen of *H. serratus*.

**Material examined.** The holotype.

**Description** (sex not known). Shell (Fig.7E,F) straight, conical, somewhat irregularly coiled, transparent and smooth with large aperture. Larval shell (Fig.12H) consisting of about 2.5 slightly convex whorls, height 0.42 mm. Holotype with 8.4 convex teleoconch whorls, constricted at subsutural zone, smooth except for some very weak and fine spiral microstriation, and some irregular incremental lines. Teleoconch with 4 incremental scars 3, 5, 6, and 7 whorls from the larval shell, plus several additional thickenings similar to scars but not marked with a furrow. Aperture is large, broad and expanded. Parietal wall evenly curved and outer lip prosocline with upper part more strongly curved, most projecting at uppermost one fifth.

**Dimensions.** Height of the holotype 8.3 mm.

**Remarks.** *Hypermastus obliquistomum* resembles *H. colmani* and *H. echinodisci* in having distinctly convex whorls, a slightly irregularly shaped aperture and a conical shape. However, the larval shell is larger and has more whorls than in *H. echinodisci* and the aperture is much smaller than in *H. colmani*, where its height is about 35% of the total height of the shell compared with 31% in *H. obliquistomum*.

### *Hypermastus peronellicola* (Kuroda & Habe, 1950)

Figs7G,H,12B

*Balcis peronellicola* Kuroda & Habe, 1950: 60.

**Type material.** One SYNTYPE (Figs 7G,H,12B) NSMT 39847.

**Type locality.** Yura Bay, Wakayama Pref., Honshu, on *Peronella leseuri*.

**Material examined.** One syntype.

**Distribution.** Southern Japan (Habe, 1976).

**Remarks.** This species was described from *Peronella leseuri* (A. Agassiz) and recorded from three other south Japanese localities. We have examined a syntype, which is somewhat similar to *H. colmani*, but has flatter whorls and a smaller and less expanded aperture.

### *Hypermastus placentae* n.sp., Warén & Crossland

Figs7I–L,8A–C,11C,D,F,13L

**Type material.** HOLOTYPE (Fig.7I-J) AMS C160817; numerous SYNTYPES AMS C160818, BMNH 1989154, USNM 860501, SMNH 4120, all from type locality.

**Type locality.** On *Arachnoides placenta* (Linnaeus, 1758), Queensland, 6 km north-north-west of Townsville, Pallarenda Beach, 19°12'S 146°47'E, lower part of intertidal sandflat, leg. M.R. Crossland.

**Material examined.** The types and Port Douglas, northern Queensland, on *Arachnoides placenta*, 6 females,

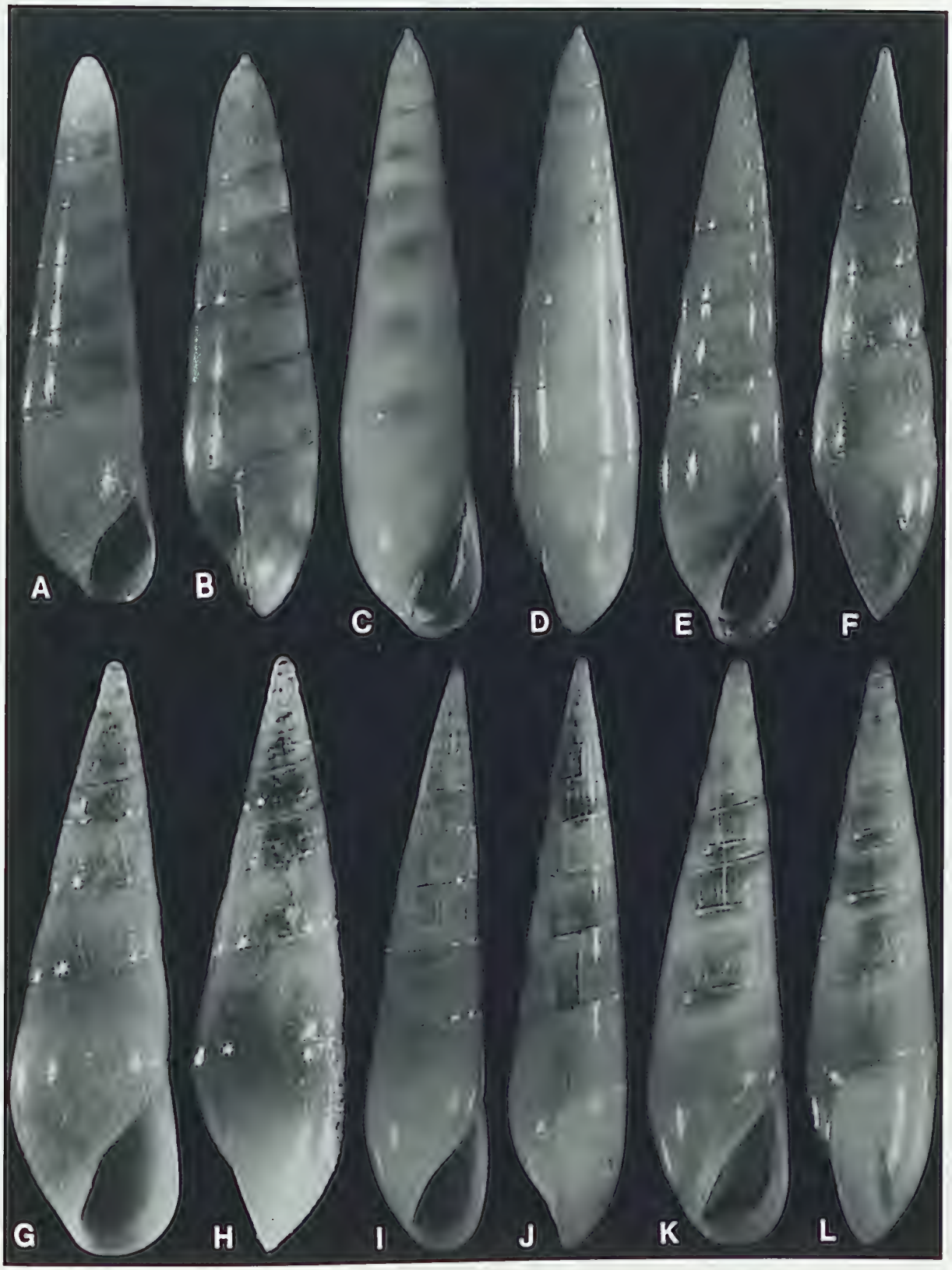


Fig.7. A–D. *Hypermastus mucronata*. A–B. syntypes, 11.4 and 10.5 mm. C–D. Sow and Pigs Reef, Sydney, New South Wales, 10.8 mm. E–F. *H. obliquistomum*, holotype, AMS C117611, 8.3 mm. G–H. *H. peronellicola*, syntype (young ?), NSMT 4.32 mm. I–L. *Hypermastus placentae*. I–J. holotype, 7.89 mm. K–L. paratype, (male) SMNH 4120, 4.29 mm.

8 males, AMS C120754.

**Description.** Shell (Figs 7I-L,8A-C) tall, straight, solid, smooth, conical with fairly large aperture. Larval shell (Fig.13L) consisting of about 1.5 slightly convex whorls height 0.36 mm. Holotype with 9.8 very flat and smooth teleoconch whorls, with some hardly perceptible and very indistinct traces of spiral lines and slightly more distinct incremental lines. Teleoconch with 10 rather strong, straight incremental scars, more distant on apical whorls, more crowded at half grown size and about 1 whorl apart on lower 4 whorls. Suture is very shallow and indistinct. False suture distinct, occupies two sevenths of the height of the whorls. Aperture rather broad, outer lip prosocline, evenly curved, and retracted at suture.

**Dimensions.** Height of holotype 7.89 mm.

**Male** (Figs 7K,L, 8A). 0.59 times height of female, with slightly more slender shell.

**Remarks.** *Hypermastus placentae* resembles *H. boschorum*, but is broader than that species and the upper part of the outer lip is not constricted in *H. boschorum*. The shape closely resembles that of *H. tenuissimae*, but that species has one whorl more in the larval shell and its surface is rougher with distinct spiral sculpture.

Crossland *et al.* (in press) have described the biology of *H. placentae* in some detail. This is summarised under "Biology". The sexes are separate, with females 1.6 times the shell height of the males. The height and sex distribution is shown in Table 3, where a set of values of specimens sexed from shell morphology is also shown.

### *Hypermastus productus* (Sowerby, 1894)

Fig.8D,E

*Eulima producta* Sowerby, 1894: 156 (not *Leiostraca producta* Carpenter, 1863: 357, new name for *Leiostraca solitaria* Carpenter, 1857: 439).

**Type material.** HOLOTYPE (Fig.8D,E) in BMNH.

**Type locality.** Hong Kong Harbour, 13-20 m. Host species unknown.

**Material examined.** The holotype.

**Distribution.** No reliable additional records exist.

**Remarks.** At a height of 30.5 mm, this is the largest species known of *Hypermastus*. We have seen no additional material and it has not been mentioned in the literature.

It should be possible to recognise *H. productus* by the very slender spire and the large height, but there is a possibility that it is the female of *H. epeterion* or *H. epiphanes*. The larval shell of the type and only known specimen is broken.

*Hypermastus productus* comes very close to being a homonym of *Leiostraca producta* Carpenter, 1863 since *Leiostraca* is an junior synonym of *Eulima*. *Leiostraca producta*, however, belongs to *Melanella* and no renaming will be necessary.

### *Hypermastus randolphi* (Vanatta, 1900)

Fig.8H,I

*Eulima randolphi* Vanatta, 1900: 256.
*Melanella* (*Melanella*) *randolphi*.–Bartsch 1917: 312.
*Melanella* (*Melanella*) *californica* Bartsch, 1917: 313.

**Type material.** *Eulima randolphi*, SYNTYPES ANSP 73729, BMNH 1929.6.6.56-59 (Fig.8H); *M. californica*, HOLOTYPE USNM 56911.

**Type locality.** *Eulima randolphi*, Unalaska Island, Alaska; *M. californica*, Catalina Island, California. Host species unknown.

**Material examined.** The material listed by Bartsch (1917).

**Distribution.** Alaska to California, usually in shallow water, 0-50 m (Bartsch, 1917).

**Remarks.** The types of the two names mentioned in the synonymy have been compared side by side and no difference could be seen.

The short, stout shell of *H. randolphi* looks quite different from most species of *Hypermastus*, but the aperture shows some similarity and there is no other group where it fits better. The larval shell consists of slightly more than one whorl and is 1.2 to 1.4 mm high. It has a diameter of 1.1 to 0.9 mm and *H. randolphi* must have very large and yolk-rich eggs. This may be a part of the reason why *H. randolphi* looks different, since a coiling starting with a large and irregular protoconch often gets a different appearance (Warén, unpublished).

A possible host for *H. randolphi* (if it really belongs to *Hypermastus*) is *Dendraster excentricus* (Eschscholtz, 1829) (Scutellidae), which is the only sand dollar common from Lower California to Alaska, in 0 to 90 m (Mortensen, 1948).

### *Hypermastus sauliae* Warén, 1980

Figs 8F,G, 13K

*Hypermastus sauliae* Warén, 1980: 291.

**Fig.8.** A–C. *Hypermastus placentae*. A. male, AMS C120754, 4.0 mm. B-C. females, AMS C120754, 7.04 mm and 6.56 mm. D–E. *H. producta*, holotype, 30.5 mm. F–G. *H. sauliae*, USNM 775663. F. female, aperture slightly damaged, 5.5 mm. G. male, 2.80 mm. H–I. *H. randolphi*. H. syntype, BMNH 1929.6.6.56-59, 7.5 mm. I. Alaska, SMNH, 7.8 mm.

**Type material.** HOLOTYPE 275267 and several PARATYPES, ANSP 349453.

**Type locality.** Tanjong, Aru, Jesselton, Sabah (North Borneo), on *Echinodiscus bisperforatus*.

**Material examined.** The type material and Bangan Bay, Kudat River, Sabah (North Borneo), from 45 *Echinodiscus bisperforatus*, leg. P. Bouchet 8 Jan. 1981, 3 females, 6 males, MNHN; Merang Beach, Trenganu State, Malaysia, 5°32'03"N 102°56'08"E, from "sand dollars", leg. T.E. Yancey 13 Aug. 1974, 1 female, 19 males, USNM 778633; 20 miles south of Klang, Selongor State, Malaysia, 2°43.5'N 101°27.3'E, from *Echinodiscus bisperforatus*, leg. T.E. Yancey 10 May 1974, 3 males, USNM 853990; Tanjong Aru, Jesselton, Sabah (North Borneo), leg. M.Saul, 1 specimen MNHN, 20 specimens, SMNH, 48 specimens, ZMA.

**Distribution.** Only known from the material examined.

**Remarks.** This species is very similar to *H. boschorum*, but that species has a more constricted outer lip and about half a whorl less in the larval shell.

### *Hypermastus serratus* n.sp., Warén

Figs 9A,B, 12C

**Type material.** HOLOTYPE (Figs 9A,B,12C) AMS C117611.

**Type locality.** "From sand dollars", Baie des Isoles, Noumea, New Caledonia, mudflats, ventral side of host, leg. P.H. Colman 15 May 1971.

**Material examined.** Only known from the holotype.

**Description** (sex not known). Shell (Fig.9A,B) cylindrical, tall, slender with sharply set off larval shell, glossy and transparent with fairly large and slender aperture. Larval shell (Fig.12C) consisting almost 2 slightly convex whorls. First teleoconch whorl partly covers larval shell and makes it difficult to measure height; estimated to 0.21-0.24 mm. First 2 teleoconch whorls increase their diameter very rapidly. Holotype with 10.3 slightly convex teleoconch whorls with occasional, almost imperceptible traces of distant spiral lines and growth lines covering upper part of subsutural zone and giving it a crenulated appearance. These lines stop abruptly after 0.05-0.1 mm. Four rather strong and deep incremental scars 5.7, 6.7, 7.7 and 9.0 whorls from larval shell. Aperture large and the parietal wall with weak angle just above midpoint of height. Outer lip retracted at suture, slightly prosocline and evenly curved.

**Dimensions.** Height of holotype 8.7 mm.

**Remarks.** This species closely resembles *H. auritae*, but differs in having the first two postlarval whorls abruptly increasing their diameter, while in *H. auritae* they are slowly and regularly increasing. It also differs from *H. auritae* in having about half a whorl more in the larval shell despite their similar height.

### *Hypermastus tenuissimae* n.sp., Warén

Figs 9C–E, 10C,D, 11A,B, 12G

**Type material.** HOLOTYPE (Fig.9C) (female?) in ZMC; 3 PARATYPES, SMNH 4121, all from type locality.

**Type locality.** West side of Ko Yao Yai, Phuket, Thailand, underside of sand dollars, *Echinodiscus tenuissimus* (L. Agassiz, 1847) (Scutellidae), leg. 5th Thai-Danish Expedition, station 1132, 21 Feb. 1966.

**Material examined.** The types and 1 male, 5.0 mm, which was sectioned and 1 male 3.9 mm (Fig.9E) which was lost after the photo was taken.

**Description** (sex uncertain, assumed to be female). Shell (Fig.9C,D) rather small, straight, conical, slender, very smooth and with small aperture. Larval shell (Fig.12G) consisting of almost 3, slightly convex whorls, height 0.40 mm. Holotype with 8.2 almost flat teleoconch whorls, without spiral sculpture but with irregular incremental lines. Holotype having about 10 distinct incremental scars, somewhat more crowded at apical part. Suture very shallow and inconspicuous. False suture distinct, subsutural zone corresponding to one quarter the height of whorls. Aperture small and narrow, not constricted in upper part. Outer lip orthocline, slightly protruding at suture, very shallowly sinuated below the suture, very slightly protruding and evenly curved below sinus.

**Dimensions.** Height of the holotype 5.68 mm.

**Male** (Fig.9E). Smaller (although one sectioned specimen of 5.0 mm was male).

**Remarks.** *Hypermastus tenuissimae* is known from six specimens only, and it cannot be excluded that it reaches a larger height, perhaps 7 to 9 mm, if all the specimens known are males.

This sand dollar parasite closely resembles *H. sauliae*, but that species has one whorl less in the larval shell (height 0.32 mm) and the surface has an indistinct spiral sculpture, which is absent in *H. tenuissimae*. Otherwise they are identical. *Hypermastus boschorum* can be separated by having an indistinct spiral sculpture, the upper part of the aperture being constricted, and by having a larval shell which is 0.35 mm high and consists of about 1.8 whorls.

One specimen of the host sand dollar preserved with the specimens (Fig.10C,D) has three ventral and three dorsal holes in the test. These consist of a shallow

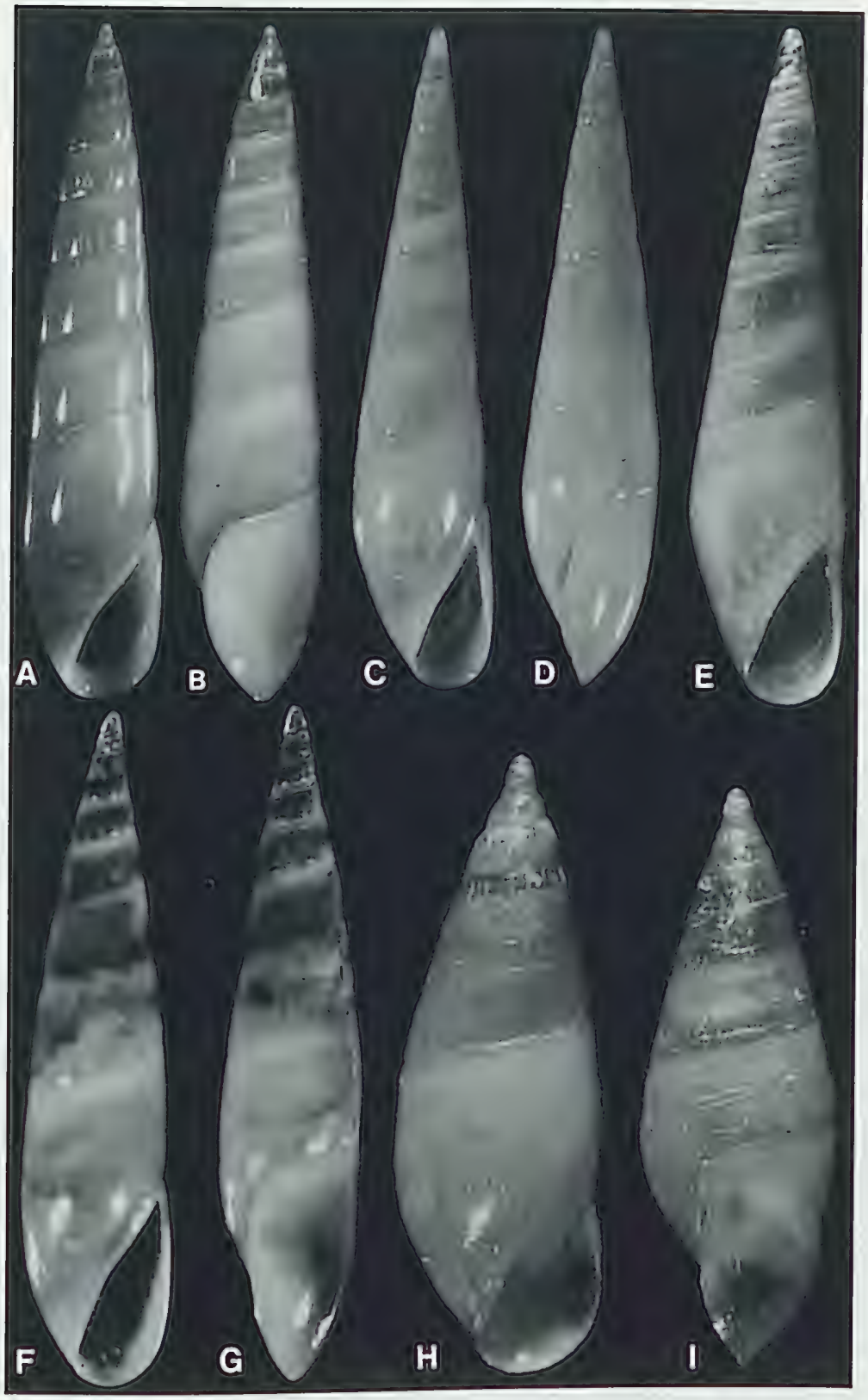


**Fig.9.** A–B. *Hypermastus serratus*, holotype, AMS 117611, 8.7 mm. C–E. *H. tenuissimae*. C–D. holotype, 5.7 mm and paratype (SMNH 4121), 5.8 mm. E. male, paratype (lost), 3.92 mm. F–G. *H. williamsi*, holotype, SAM D 10637, 6.78 mm. H–I. *Turveria encopendema*, LACM 55556, 4.20 and 3.96 mm.

pit, in the bottom of which there is a final penetration of the test (Fig.11A,B). It is not known if all the specimens in the type material come from this single host specimen, or also from additional ones.

***Hypermastus williamsi*** (Cotton & Godfrey, 1932)

Figs 9F,G, 12D

*Strombiformis williamsi* Cotton & Godfrey, 1932: 39.

**Type material.** HOLOTYPE (Figs 9F,G,12D), South Australian Museum D 10637; PARATYPE, 1 shell, South Australian Museum D 16217.

**Type locality.** St Vincent's Gulf, South Australia, 18 m. Host species unknown.

**Material examined.** The types.

**Distribution.** No reliable additional records exist.

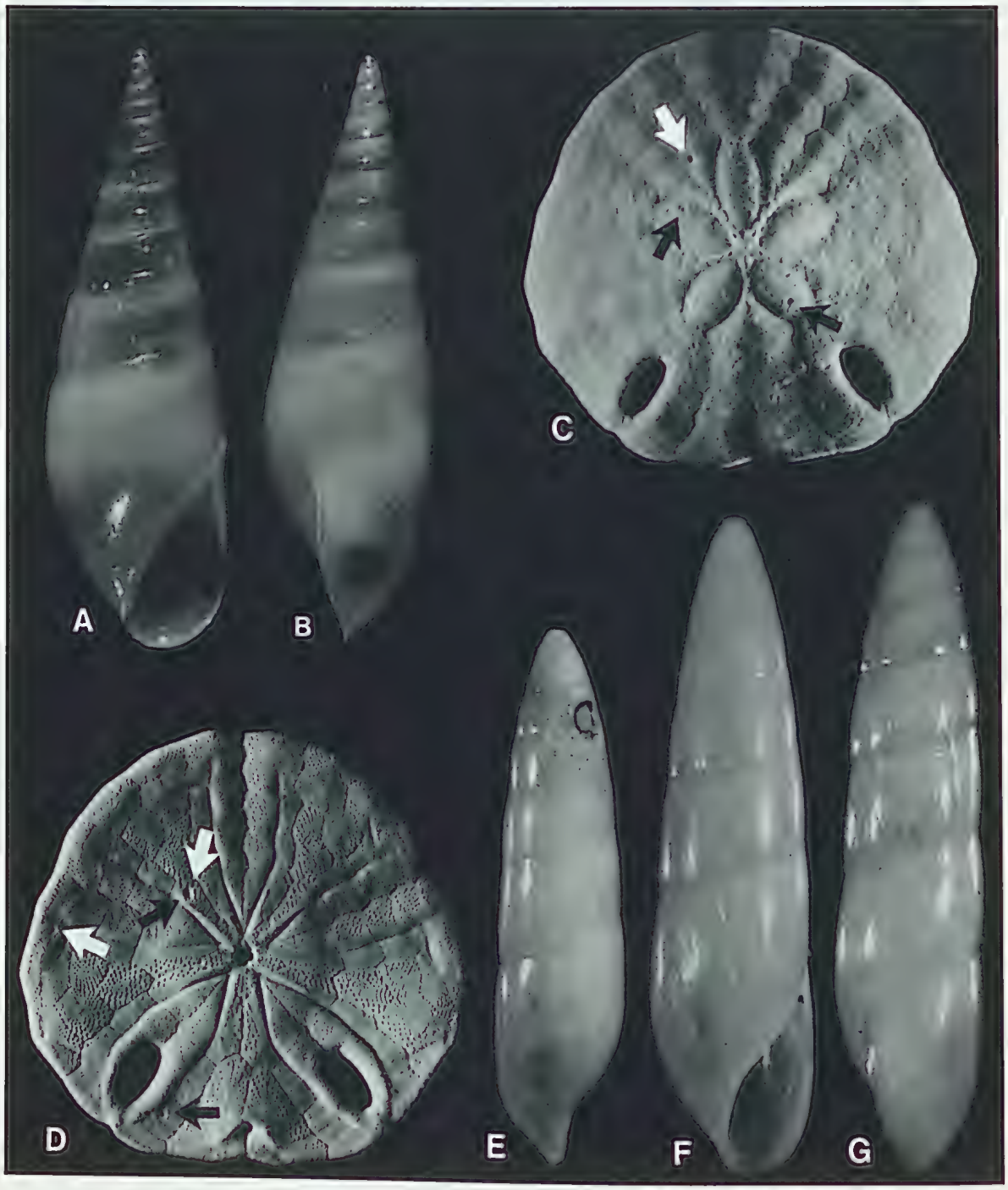


**Fig.10.** A–B. *Turveria schwengelae*, LACM 55553, 5.23 and 5.06 mm. C–D. *Echinodiscus tenuissimus*, parasitised by *Hypermastus tenuissimae*, scars indicated by arrows. Diameter of host 37 mm. E. *Eulima philippiana*, holotype, 10.4 mm. F–G. *Eulima dunkeriana*, syntypes, ANSP 80637, 10.5 and 12.1 mm.

**Remarks.** The position in *Hypermastus* is concluded solely from shell characters.

*Hypermastus williamsi* can be recognised from the larval shell (Fig.12D) which is less cylindrical than normal and consists of more than two whorls (height 0.55 mm). The larval development is probably planktotrophic.

### *Turveria* Berry, 1956

**Type species.** *Turveria encopendema* Berry, 1956, by original designation, Mexico, Baja California, on *Encope grandis* L. Agassiz, 1841 and *E. californica* Verrill, 1870 (Scutellidae).

**Description.** Medium sized (4-6 mm) eulimids parasitic on sand dollars, with a rather short and broad, conical, shell with a reddish brown colour pattern. Surface covered by a very fine but distinct sculpture of axial lines. Aperture small and narrow with the line columella-parietal wall almost straight. Outer lip slightly sinuated below the suture.

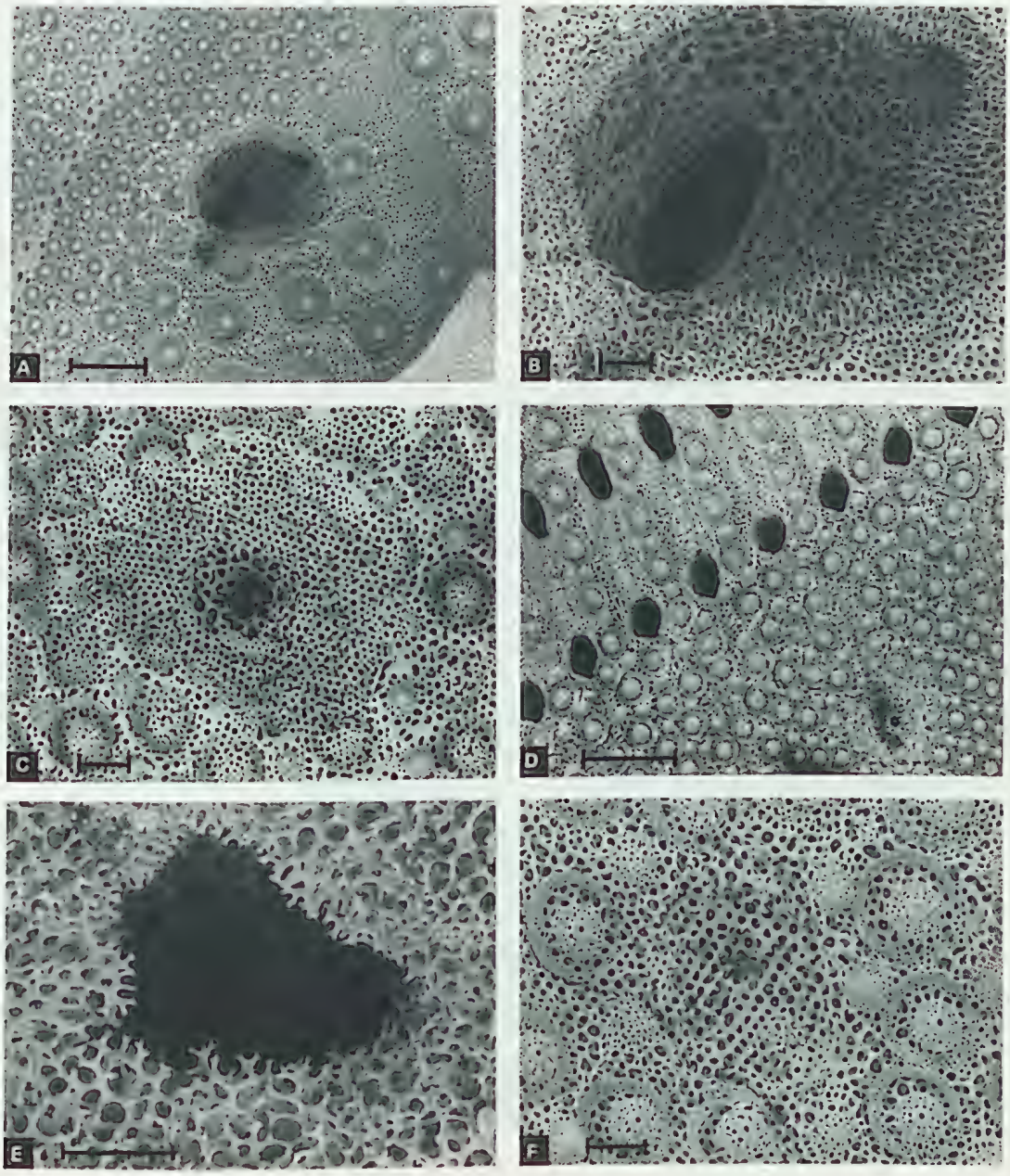


**Fig.11.** Holes in tests of sand dollars, caused by *Hypermastus* spp. A–B. *Echinodiscus tenuissimus*, parasitised by *H. tenuissimae*. Notice that there are two penetrations by the proboscis. Notice also the pointed structure of the skeletal network which indicates that the hole has been caused by dissolution of the skeleton. C–D. Arachnoides placenta, parasitised by *H. placentae*. C. Shallow attachment. D. Deeper attachment. E. *Echinodiscus bisperforatus*, parasitised by *H. boschorum*. F. *Arachnoides placenta* parasitised by *H. placentae*. Shallow attachment. Scale lines A, D, 0.5 mm; B, C, E, F, 0.1 mm.

**Remarks.** As mentioned in the introduction, the species of *Turveria* are characterised by having a shell with colour spots and bands, and a distinct microsculpture of dense and sharp incremental lines not occurring in any known species of *Hypermastus*. They also differ by having a sinuated outer lip, while that of *Hypermastus* is evenly curved or straight. Apart from this, the shells are quite similar. In a front view the shape of the aperture is very much the same,.

### *Turveria encopendema* Berry, 1956

Figs 12H,I, 13A,H

*Turveria encopendema* Berry, 1956: 156.

**Type material.** In the collection of S.S. Berry, now in SBMNH (not available).

**Type locality.** Outer strand of Cholla, Bahia de Adaur, Sonora, Mexico, on *Encope grandis* and *E. californica*.

**Material examined.** Cholla Bay, Sonora, Baja California, on *Encope grandis*, 2 specimens, LACM 55556; El Magote, La Paz Harbor, Baja California, 24°10'N 112°W, intertidal to 2.5 m, 1 specimen, no host, LACM 66-29; Bahia de Adair, Sonora, Mexico, no host, 1 specimen, 5 shells, LACM 55557; Sand flats at Willard Island, Bahia san Luis Gonzaga, Baja California, Mexico, on *Encope grandis*, 1 specimen, LACM 55554; Cholla Bay, Puerto Penasca, Sonora, intertidally down to 1 m, on *Encope grandis*, 43 specimens, coll. D. Shasky.

**Distribution.** No reliable additional records exist.

**Remarks.** It has not been possible to examine any type material and Berry's "camera lucida drawing" is too rough to be of any help and is probably based on a young specimen. Berry mentions, however, that the larval shell is mucronate, which clearly distinguishes his species from *T. schwengelae*. For further differences, see *T. schwengelae*.

### *Turveria schwengelae* (Bartsch, 1938)

Figs 10A,B, 13F,G

*Strombiformis hemphilli* Bartsch, 1917: 344.
*Leiostraca schwengelae* Bartsch, 1938: 34.

**Type material.** HOLOTYPE and 3 PARATYPES, USNM 127554.

**Type locality.** Point Abrejos, Baja California.

**Material examined.** The types and Concepcion Bay, Baja California, 26°42'N 111°55'W, 1 shell, no host, LACM 63-37; Willard Island, Bahia san Luis Gonzaga, Sonora, Baja California, on *Encope* sp., 4 specimens, LACM 55553; Bahia San Luis Gonzaga, Sonora, Baja California, on *Encope grandis*, intertidal, 36 specimens, leg. D. Shasky.

**Description** (sex not known). Shell (Fig.10A,B) conically lanceolate, solid, smooth, transparent, with brownish markings along suture and on outer lip. Larval shell (Fig.13F,G) consisting of about 2.7 distinctly convex whorls and is perfectly smooth, colourless except for an occasional brownish tint on initial whorl. Visible height of larval shell 0.26 mm, and total height of shell of larva estimated to about 0.29 mm. A specimen of 5.2 mm has 7.25 teleoconch whorls of slowly and uniformly increasing diameter, sculptured by numerous dense and sharp incremental lines. Teleoconch with 9 incremental scars, 1.2, 1.9, 2.8, 3.8, 4.3, 4.8, 5.5, 6.0 and 6.6 whorls from outer lip, but as usual there is some individual variation in this character. Suture is shallow but distinct and makes a distinct turn downwards about 0.3 mm before outer lip. Aperture is distinctly constricted in its upper part as a consequence of this, and pear shaped. Outer lip distinctly prosocline, with shallow sinus below suture. Colour pattern not as bright as in *T. encopendema*, consisting of a brownish spiral band just below periphery of body whorl. Band concealed under, or visible through subsutural zone on earlier whorls; also a large, roundedly triangular blotch at lower part of outer lip and one less distinct, sometimes absent, similar spot just below corner between outer lip and suture.

**Dimensions.** Maximum height 5.8 mm.

**Remarks.** *Strombiformis hemphilli* was renamed *Leiostraca schwengelae* because of supposed secondary homonymy with *Eulima* (*Leiostraca*) *hemphilli* Dall, 1883. *Leiostraca schwengelae* is a replacement name proposed before 1961, and thus *S. hemphilli* is permanently invalidated.

Since we have good material of this species and Bartsch's description is not easy to uinderstand, we have redescribed it. *Turveria schwengelae* differs from *T. encopendema* by having a regularly conical spire, flatter whorls, less vivid colour pattern, and by being about one fifth higher (4.91 ± S.D. 0.27 mm among 23 mature specimens; 4.18 ± S.D. 0.27 mm among 26 specimens of *T. encopendema*).

## Doubtful Species

### *Eulima philippiana* Dunker, 1860

Fig.10E–G

*Eulima philippiana* Dunker, 1860: 226.
*Eulima dunkeriana* Pilsbry, 1901: 395.

**Type material.** *Eulima philippiana*, holotype (Fig.10E) SMF, Frankfurt a. M. (ex Heidelberg no. 2773); *E. dunkeriana* (Fig.10F,G), syntypes ANSP 80637.

**Type locality.** *Eulima philippiana*, Japan, Harbour of Decima; *E. dunkeriana*, Hindo, Japan. Host species unknown.

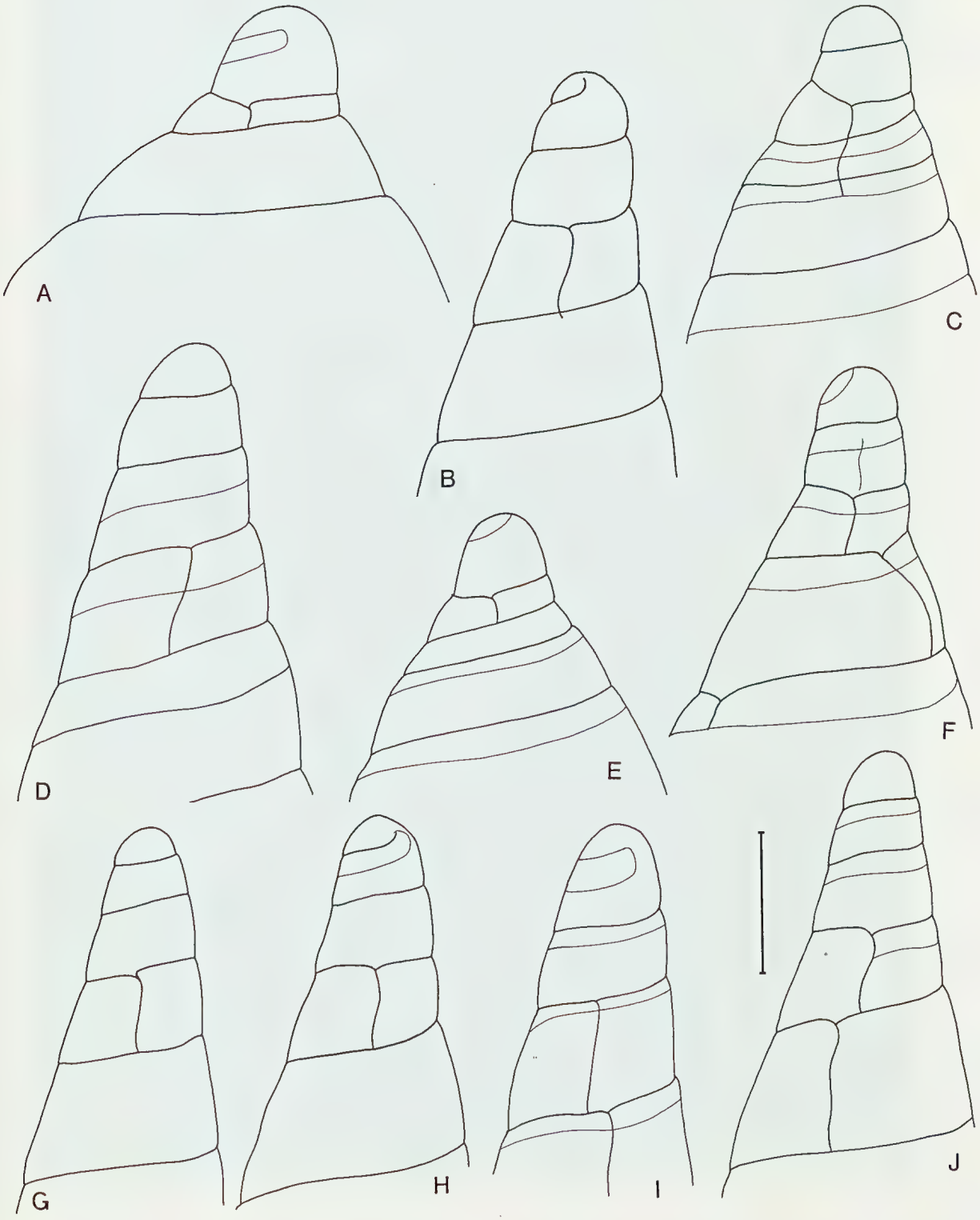


**Fig.12.** A–J. Larval shells, all at the same magnification. A. *Hypermastus georgiregis*, holotype. B. *H. peronellicola*, syntype. C. *H. serratus*, holotype. D. *H. williamsi*, holotype. E. *H. mucronata*, Sydney. F. *H. minor*, holotype. G. *H. tenuissima*, holotype. H. *H. obliquistomum*, holotype. I. *H. epepterion*, holotype. J. *H. colmani*, holotype. Scale line 0.25 mm.

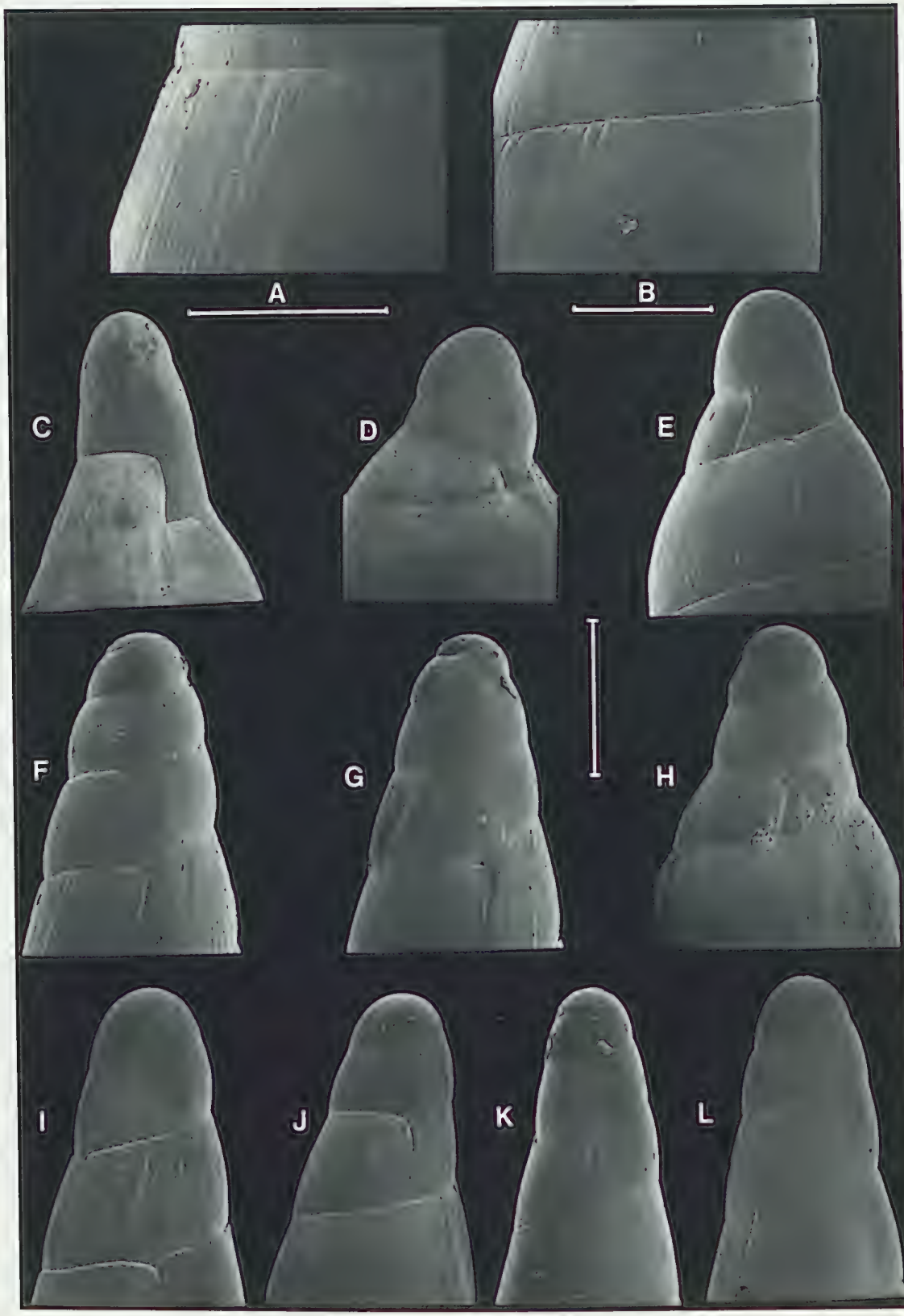


**Fig.13.** Sculpture and larval shells. A. *Turveria encopendema*, incremental lines, LACM 55557. B. *Hypermastus kilburni*, paratype SMNH 4119, sutural incremental lines. C–L. larval shells, all at the same magnification. C. *H. echinodisci* USNM. D. *H. coxi* AMS C120739. E. *H. kilburni*, paratype, SMNH 4119. F–G. *T. schwengelae*, LACM 55553. H. *T. encopendema*, LACM 55557. I. *H. auritae*, paratype, SMNH 4115. J. *H. boschorum*, paratype, SMNH 4117. K. *H. sauliae*, USNM 778633. L. *H. placentae*, paratype, SMNH 4120. Scale line 0.25 mm.

**Material examined.** The type material.

**Distribution.** No reliable additional records.

**Remarks.** The holotype of *E. philippiana* is in very poor condition. It is worn and both the apex and the aperture are broken. The holotype of *E. dunkeriana* is not much better. We are, however, convinced that they are conspecific.

Our impression is that *E. philippiana* does not belong to *Hypermastus*, since the outer lip is almost perfectly straight, forms an angle of slightly more than 90° with the suture and is distinctly prosocline. In *Hypermastus* it is usually convex, often with a small, blunt angle shortly below the suture. We are, however, not sure and figure it for comparison.

## Summary of Taxonomic Changes

The following new species are described: *Hypermastus auritae* n.sp., Warén is a parasite of *Echinodiscus auritus* from Oman; *H. boschorum* n.sp., Warén is a parasite of *E. bisperforatus*, also in Oman; *H. colmani* n.sp., Warén parasitises *Peronella leseuri* in Queensland; *H. kilburni* n.sp., Warén is described from an undetermined sand dollar in Mozambique; *H. minor* n.sp., Warén is described from *E. bisperforatus* from Malaysia; *H. obliquistomum* n.sp., Warén and *H. serratus* n.sp., Warén are described from undetermined sand dollars from New Caledonia; *H. placentae* n.sp., Warén & Crossland is described from *Arachnoides placenta* from Queensland; *H. teuissimae* n.sp., Warén is described from *Echinodiscus tenuissima* from Thailand.

Fifteen eulimids are transfered to *Hypermastus*, based on shell characters, viz.: *Eulima acuta* Sowerby, 1834 (Pacific Panama); *Eulima acuta* A. Adams, 1851 (Philippines); *Eulima bulbula* Murdoch & Suter, 1906 (New Zealand); *Leiostraca casta* A. Adams, 1861 (new synonyms *L. constantia* A. Adams, 1861 and *L. maria* A. Adams, 1861) (off northern China); *Mucronalia cylindrica* Sowerby, 1900 (Philippines); *Eulima epeterion* Melvill, 1889 (Mauritius); *Eulima epiphanes* Melvill, 1897 (Persian Gulf); *Eulima georgiregis* Cotton & Godfrey, 1932 (South Australia); *Eulima indistincta* Thiele, 1925 (Sumatra); *Eulima mucronata* Sowerby, 1866 (South Australia and New South Wales); *Leiostraca schwengelae* Bartsch, 1938; *Balcis peronellicola* Kuroda & Habe, 1950 (Japan); *Eulima producta* Sowerby, 1894 (Hong Kong); *Eulima randolphi* Vanatta, 1900 (new synonym: *Melanella californica* Bartsch, 1917) (Alaska); and *Eulima williamsi* Cotton & Godfrey 1932 (South Australia). *Eulima philippiana* Dunker, 1860 is a valid senior synonym of *Eulima dunkeriana* Pilsbry, 1901 and the systematic position of the species is uncertain.

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A special thanks is directed to Dr D. Bosch, Clover, South Carolina, who spent much time collecting eulimids from sand dollars and to Dr D.R. Shasky, Redlands, California who contributed most specimens of the genus *Turveria*.

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## APPENDIX 1

Table 1. Height and sex distribution of *Hypermastus auritae*.

| | male | female |
|---|---|---|
| number | 31 | 10 |
| max height mm | 7.9 | 12.3 |
| min height mm | 6.2 | 10.4 |
| mean height mm | 7.0 | 11.2 |
| S.D. mm | 0.5 | 0.6 |

Table 2. Height and sex distribution of *Hypermastus boschorum*.

| | male | female |
|---|---|---|
| number | 14 | 13 |
| maximum height mm | 4.64 | 6.39 |
| minimum height mm | 4.02 | 5.07 |
| mean height mm | 4.26 | 5.75 |
| S.D. mm | 0.20 | 0.46 |

Table 3. Height and sex distribution of *Hypermastus placentae*.

| | male | female | indet. |
|---|---|---|---|
| number, A.W. | 21 | 13 | |
| number, M.C. | 20 | 45 | 55 |
| maximum height, A.W., mm | 4.4 | 7.7 | |
| maximum height, M.C., mm | 7.4 | 8.1 | |
| minimum height, A.W., mm | 3.6 | 6.1 | |
| minimum height, M.C., mm | 1.8 | 4.0 | |
| mean height, A.W., mm | 4.0 | 6.8 | |
| mean height, M.C., mm | 4.2 | 6.8 | |
| S.D., A.W., mm | 0.21 | 0.41 | |
| S.D., M.C., mm | 1.69 | 0.92 | |

Comments. A.W., values based on specimens sexed according to shell morphology, by A. Warén. – M.C., based on values published by Crossland *et al.* 1990. – S.D., standard deviation

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# Redescription of *Calohelcon* Turner (Insecta: Hymenoptera: Braconidae), Description of a New Species, and a Reappraisal of the Significance of Certain Character States in the Helconinae

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ABSTRACT. *Calohelcon obscuripennis* Turner is redescribed and illustrated for the first time. *Calohelcon roddi* n.sp. from New South Wales is described, illustrated and differentiated from *C. obscuripennis*. The hindwing of *C. roddi* possesses a distinct transverse vein m-cu, a feature unknown in any other Helconinae but present in many members of the 'cyclostome' subfamilies Doryctinae and Rogadinae, and in the apparently related Alysiinae, Betylobraconinae, Gnamptodontinae, Histeromerinae, Opiinae and Telengaiinae. The presence of hindwing vein m-cu is interpreted as a plesiomorphous character state in the 'cyclostome' assemblage, but it is suggested that the presence of m-cu in some *Calohelcon*, represents a re-expression of genetic information, the expression of which had been previously suppressed. The phylogenetic significance of a number of other features of *Calohelcon*, and of Helconinae in general, are discussed.

QUICKE, D.L.J. & G.A. HOLLOWAY, 1991. Redescription of *Calohelcon* Turner (Insecta: Hymenoptera: Braconidae), description of a new species, and a reappraisal of the significance of certain character states in the Helconinae. Records of the Australian Museum 43(2): 113–121.

Recently major advances have been made in our understanding of the phylogenetic relationships between the subfamilies of Braconidae (Capek, 1970; van Acterberg, 1984; Sharkey, personal communication), although there is as yet no clear consensus of opinion, and several subfamilies are problematical. Application of Hennigian cladistics (Hennig, 1966) has proved invaluable in that by consistently differentiating between

synapomorphies and symplesiomorphies, a robust classification can be achieved and where necessary, the limits of subfamilies redefined (van Achterberg, 1976, 1979a-c, 1983b; Quicke, 1987). As a result of this work, a considerable effort has been put into finding new phylogenetically significant characters, and one that has been highlighted recently as being of considerable potential importance is the presence or absence of the transverse hindwing vein m-cu (Sharkey, 1988, personal communication). Hindwing vein m-cu occurs in the Doryctinae and Rogadinae, and in the apparently related subfamilies Alysiinae, Betylobraconinae, Gnamptodontinae, Histeromerinae, Opiinae and Telengaiinae. Importantly, its loss appears to be absolute in other braconid lineages with the single exception of the helconine genus *Calohelcon* Turner that is redescribed below. The significance of this and other character states displayed by *Calohelcon* are discussed.

The Australian genus *Calohelcon* has not been published on since its original description by Turner (1918), apart from its inclusion in subsequent catalogues, and it has never been illustrated. *Calohelcon* belongs to the tribe Helconini (see van Achterberg, 1976a, 1984) having forewing vein 1r-m present, having forewing vein 2-SR+M longitudinal (i.e. vein m-cu is inserted into the first rather than the second submarginal cell), and having both forewing veins 1A and 2A. However, *Calohelcon* is aberrant in several features, largely associated with a reduction of body sculpture, viz. the propodeum is smooth and not differentiated from the posterior part of the metapleuron, the first metasomal tergite lacks both dorsal and dorsolateral carinae and the precoxal suture is absent. The discovery of additional material of *Calohelcon* in both the Australian Museum and in the Australian National Insect Collection and the inadequacy of its original description in failing to mention many of its unique features, prompted us fully to redescribe and illustrate this interesting and uncommon Australian braconid genus.

Terminology follows that of van Achterberg (1979c). Figures are shaded as if illuminated from the upper right. Collections are abbreviated as follows: AM – Australian Museum; ANIC – Australian National Insect Collection; BMNH – British Museum (Natural History).

## Redescription

### *Calohelcon* Turner

*Calohelcon* Turner, 1918: 163, 165.

**Type species.** *Calohelcon obscuripennis* Turner, 1918 (monobasic).

**Additional species.** *Calohelcon roddi* n.sp.

**Diagnosis.** Moderately large braconid wasps with wingspans greater than 2 cm. Maxillary and labial palps with 6 and 4 segments respectively. Antennal sockets with protruding lateral margin. Malar suture absent. Malar space large. Frons with a well-developed midlongitudinal carina. Eyes glabrous, not emarginate. Hypostomal and occipital carinae complete and lamelliform or the occipital carina largely reduced. Mesosoma smooth and shiny. Pronotum with a crenulate groove anteriorly. Propleuron with a lateral carina. Median lobe of mesoscutum not depressed relative to lateral lobes. Precoxal suture absent. Mesopleural suture crenulate. Propodeum without carinae, largely glabrous; not differentiated from the metapleuron. Propodeal spiracle small and eliptical. Metapleuron with a well-developed flange. Forewing with costal cell distinct for more than half length from tegula to pterostigma. Forewing with veins 1r-m, 2A and 3-1A. Hindwing with veins C and 2A well-developed; vein m-cu represented by a least a spur arising from 2-M; without veins r and r-m. Claws simple with small, rounded, non-pectinate basal lobes. Hind trochanter not slender. Hind femur smooth ventrally, without rugae. Metasoma smooth and shiny. First metasomal tergite large; without dorsal or dorsal-lateral carinae; strongly bulbously produced on each side anterodorsally. Ovipositor approximately as long as the body; with a preapical dorsal, circular notch in lateral aspect. Venom gland reservoir thin walled and weakly muscularised (Type II of Edson & Vinson, 1979).

**Description.** Terminal flagellomere pointed but not acuminate. All flagellomeres longer than wide. Lower margin of clypeus carinate, forming a narrow transverse 'hypoclypeal depression'. Clypeus distinctly differentiated from the face by a groove. Face broadly setose medially; with a midlongitudinal raised area. Antennal sockets margined by a flange laterally. Frons depressed, with a well-developed midlongitudinal carina.

Pronotum with a small pronope formed by the submedial pair of carinae. Notauli moderately well developed, not crenulate. Median lobe of mesoscutum distinctly protruding over the pronotum. Anterior scutellar sulcus broad and crenulate. Scutellum with a submarginal, posterior row of pits. Epicnemial area smoothly impressed, without sculpture. Episternal scrobe absent. Median area of metanotum with a medial and a pair of lateral anteriorly diverging carinae. Propodeum not differentiated from metapleuron.

*Forewing.* Costal cell narrow but distinct for at least the apical half of vein C. Second submarginal cell short. Vein r-m moderately curved, with one posterior bulla. Vein 1-SR+M sigmoid, with or without a short posteriorly directed spur. Vein 2-SR+M longitudinal. Vein cu-a postfurcal. Vein 1A reclivous.

*Hindwing.* Vein C well developed, without especially thickened bristles apically (see Quicke, 1982). Costal cell distinctly though weakly sclerotised posteriorly. Vein 2-SC+R longitudinal, without distinct large, erect bristle(s). Anterior margin of wing reaching vein SC+R1 considerably before the hamuli proper (= distal hamuli).

Vein R1 with 8 to 10 hamuli, the basal 3 being somewhat larger than the remainder. Vein M+CU much longer than 1-M. Vein m-cu sometimes represented by a short spur or a distinct short vein arising from near the base of vein 2-M. Vein cu-a approximately perpendicular to 1-M. Plical cell moderately large. Vein 2-A well developed. Setosity of wing membrane considerably less dense basally than apically.

Claws with a small rounded basal lobe, without pectination. Legs moderately slender. Tarsi without an obvious midventral, longitudinal row of setae.

Metasoma smooth and shiny, largely glabrous; inserted above hind coxae. First tergite large, without dorsal or dorsolateral carinae, strongly bulbously swollen on either side, anterodorsally; with a distinct laterope. First spiracle small. Laterotergites of all tergites well developed. Spiracles of tergites behind the first, in the laterotergites. Sternites largely sclerotised though less strongly so medially and posteriorly. Hypopygium small. Ovipositor approximately as long as the body, distinctly curved dorsally expect for the apex; with a weak preapical dorsal notch or a small, almost circular (in lateral aspect) dorsal hollow with apicoventral serrations.

**Biology.** Helconines are usually koinobiont endoparasitoids of concealed coleopterous larvae (Gauld & Bolton, 1988). However, one specimen of *C. obscuripennis* bears a label that it was "probing tree trunks with cossid larvae", and although this is hardly a confirmed record it does suggest that *Calohelcon* species may actually be parasitoids of Lepidoptera rather than Coleoptera larvae.

## Key to the Species of *Calohelcon*
(females only)

1. First metasomal tergite constricted submedially in dorsal aspect (Fig.1a); mesoscutum and metasomal tergites 5-9 black; wings yellowish on basal half, grey-brown apically ..... *C. obsuripennis*

—— First metasomal tergite not constricted submedially in dorsal aspect (Fig.3f); mesoscutum and metasomal tergites 5-9 orange; wings more or less evenly light brown ..... *C. roddi* n.sp.

### *Calohelcon obscuripennis* Turner

Fig.1

*Calohelcon obscuripennis* Turner, 1918: 165.

**Material examined.** HOLOTYPE female (BMNH, 3c 901): "Australia. R.E. Turner. 1909 - 220.", "*Calohelcon obscurpennis* Type Turn. ". "B.M. TYPE HYM. 3.c. 901" & "Type H.T.". PARATYPE male (BMNH): "c7.2.01 Victoria", "Australia R.E. Turner 1909 - 220" & "*Calohelcon obscuripennis* cotype Turn.".

1 female (ANIC): "Bonville NSW 23 Aug. 1977 R.S. McInnes & J Green. Probing tree trunks with cossid larvae"; 1 female (BMNH) - no data.

**Description.** *Females.* Length of body 14.0-14.5 mm, of forewing 14.0-15.0 mm, of ovipositor (part extended beyond the metasomal tergites) 16.5-19.0 mm and aof antenna (broken in holotype) 16.0 mm.

Antenna with 47 flagellomeres, slightly longer than the forewing. Terminal flagellomere partially fused to the penultimate flagellomere. Median flagellomere parallelogram-shaped in profile; 1.35 x longer laterally than wide. First flagellomere 1.2 x longer than both the 2nd and 3rd separately, the latter being 2.2 x longer than maximally wide. Ratios of height of clypeus: intertentorial distance: tentorio-ocular distance = 17:26:30. Malar space 0.61 x height of eye. Ratio of height of eye: width of face: width of head = 41:69:112. Facial ridge densely punctuate, bordered laterally by grooves. Antennal sockets with crenulate margins anteriorly and laterally. Frons largely without carinae except anteriorly. Ratios of distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 12:8:27.

Mesosoma 1.6-1.68 x longer than high. Scutellar sulcus with 5-6 transverse crenulae. Scutellum sometimes with a short midlongitudinal row of fine pits.

*Forewing.* Ratios of length of veins r:3-SR: SR1 = 23:28:135. Ratios of lengths of 2-SR: 3-SR : r-m = 34:28:29. Vein m-cu 1.57 x longer than shortest distance between 1st discal cell and 2nd submarginal cell. Vein 3-CU1 very weakly expanded posteriorly.

*Hindwing.* Vein M+CU 2.73 x longer than 1-M. Vein R1 with 9 hamules.

Ratios of lengths of fore femur: tibia: tarsus = 21:25:25. Fore basitarsus 5.7 x longer than maximally deep. Ratios of lengths of hind femur: tibia: tarsus = 29:52:14. Hind basitarsus 5.4 x longer than deep. Hind femur 4.5 x longer than deep. Inner hind tibial spur 0.28 x length of basitarsus.

First metasomal tergite approximately as long as maximally wide; distinctly narrowing behind the

basodorsal lobes. Second tergite 3.0 wider than long.

Largely black; the head largely yellow except for a mark on the stemmaticum and the centre of the frons; posterior third of propodeum, posterior half of metapleuron, first tergite except for a medial mark subposteriorly, ivory white. Basal half of both wings yellowish becoming gradually grey-brown apically; venation brownish (paler basally); pterostigma brown except for a small yellowish mark basally.

### *Calohelcon roddi* n.sp.

**Type material.** Female HOLOTYPE and PARATYPE in the Australian Museum collected by Norman Rodd from Lane

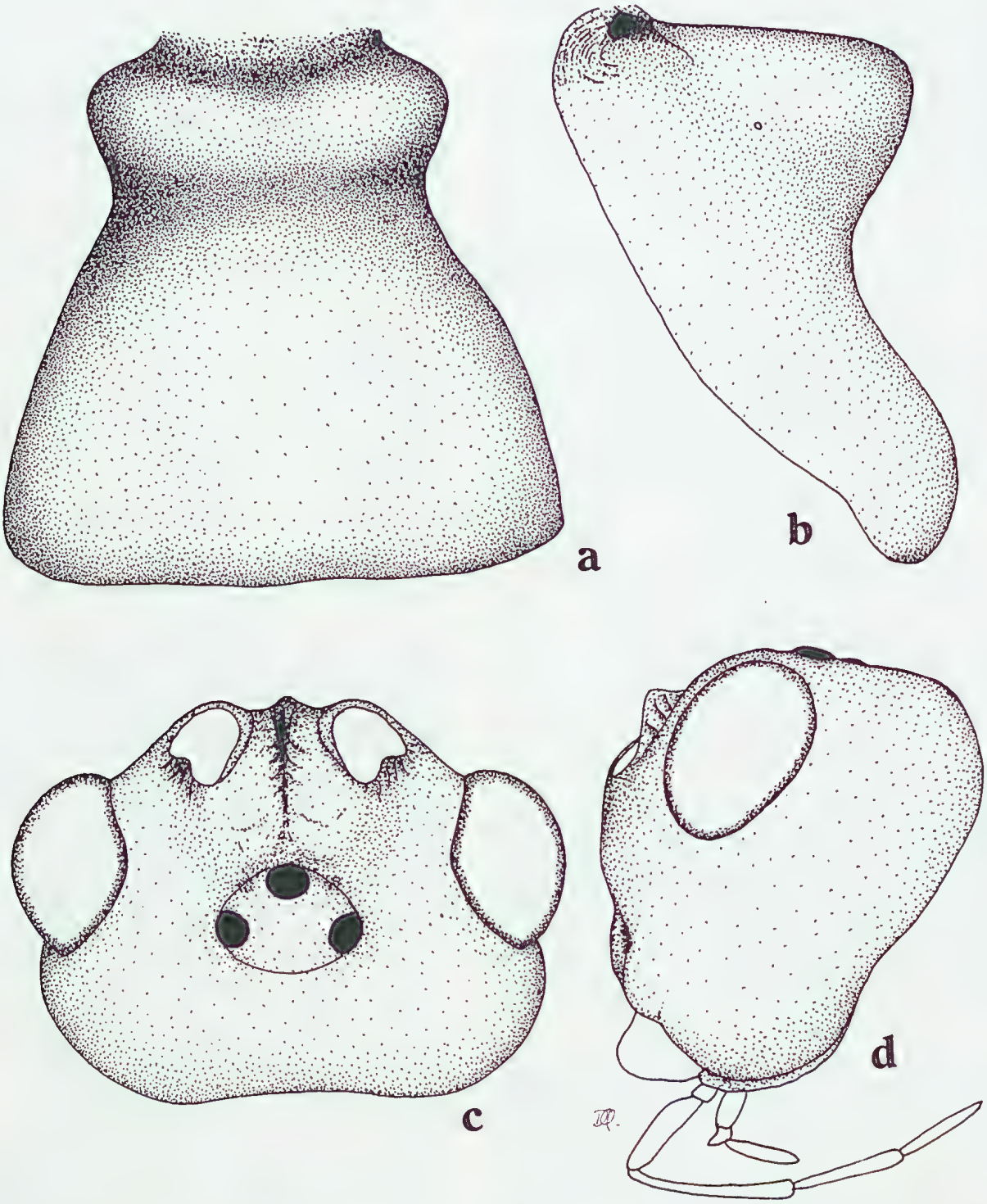


**Fig.1.** *Calohelcon obscuripennis* Turner, female: a, first metasomal tergite, dorsal aspect; b, first metasomal tergite, lateral aspect; c, head, dorsal aspect; d, head, lateral aspect.

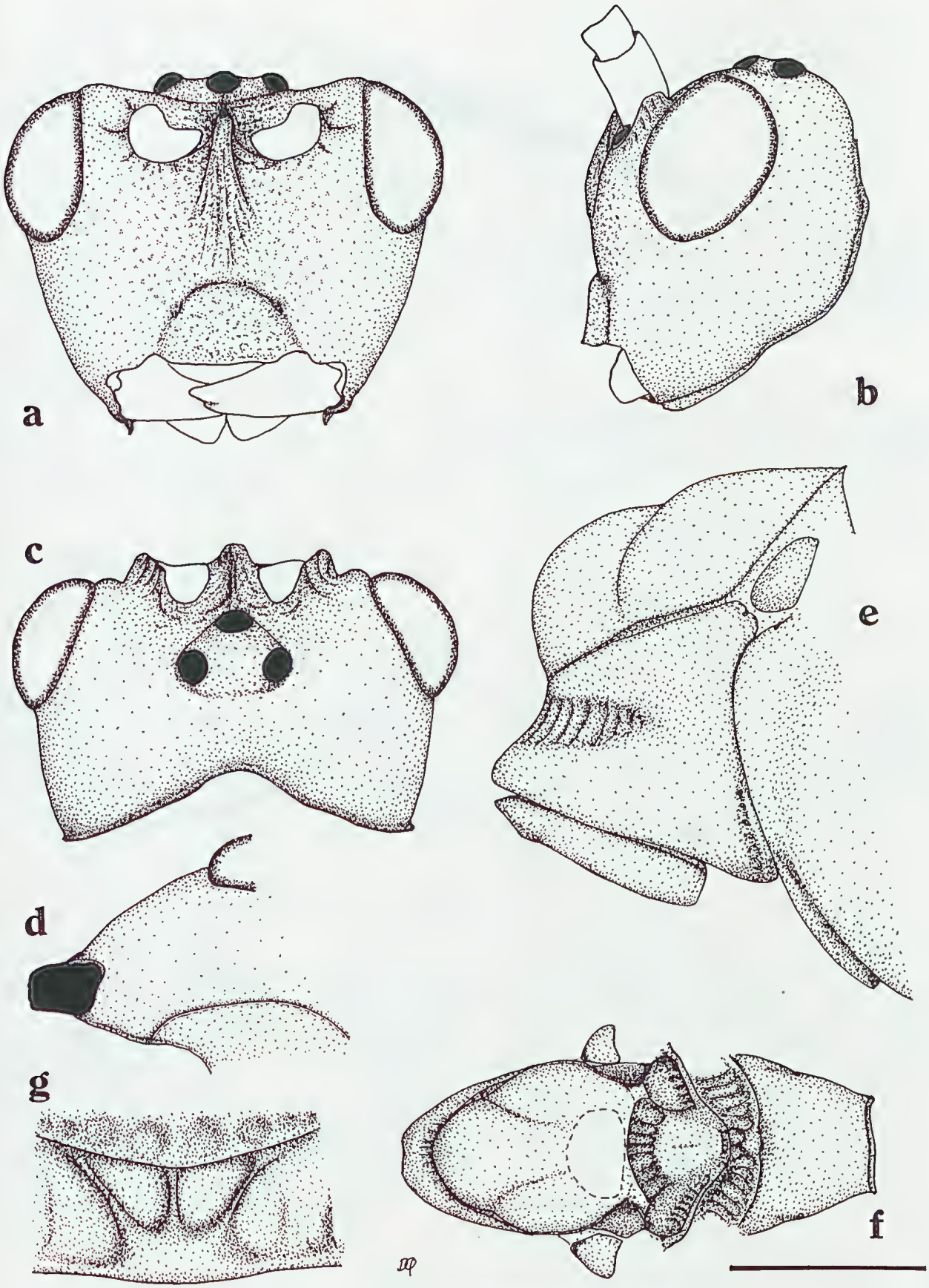


**Fig.2.** *Calohelcon roddi* n.sp., female: a, head, frontal aspect; b, head, lateral aspect; c, head, dorsal aspect; d, head, oblique aspect of posterior, lower left part (mandible black); e, anterior of mesosoma, lateral aspect; f, mesosoma, dorsal aspect; g, median area of metanotum and posterior of scutellum, dorsal aspect. Scale line a,b,c,d,e = 1 mm; f = 2.0 mm; g = 0.5 mm.

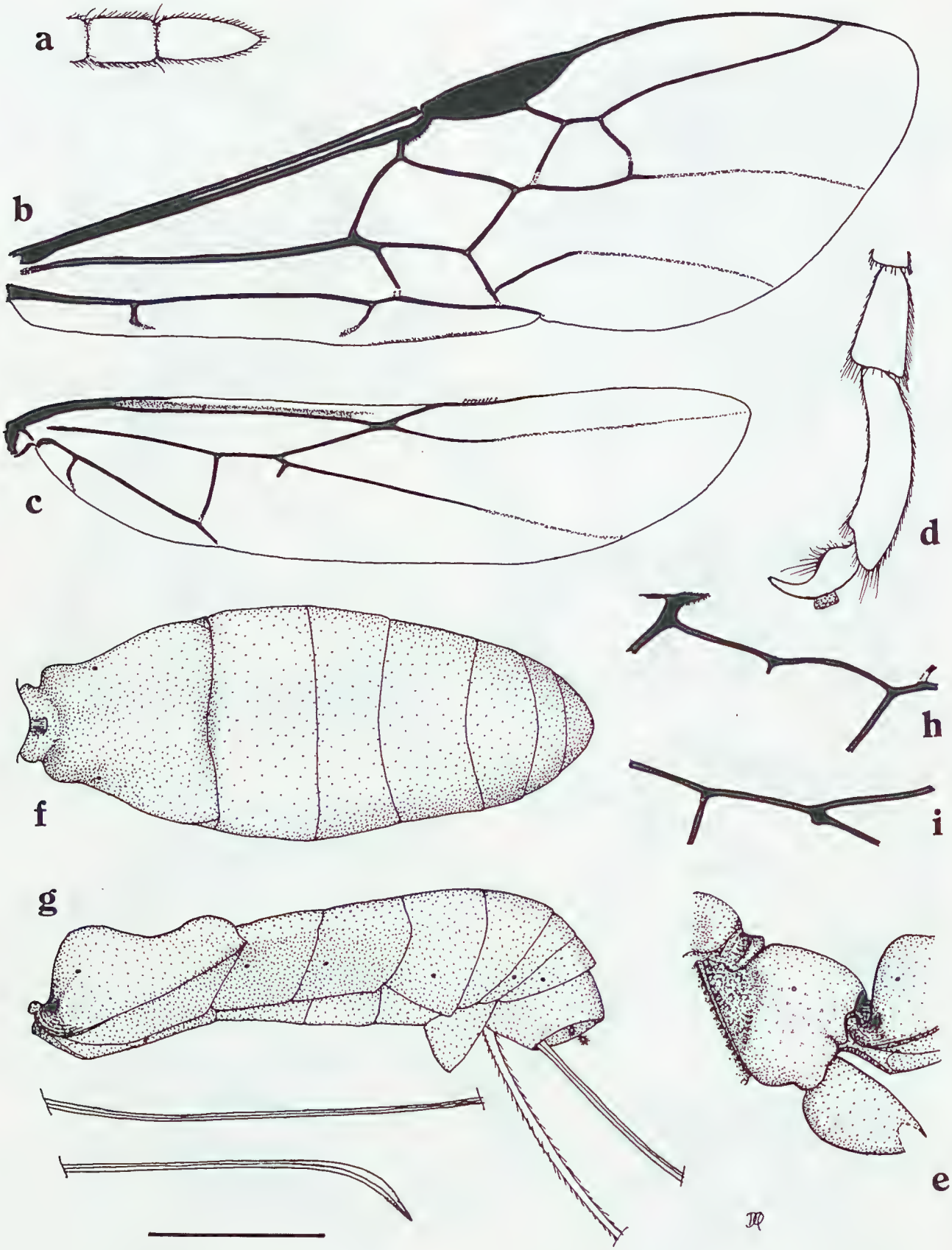


**Fig.3.** *Calohelcon roddi* n.sp., female: a, terminal 2 flagellomeres; b, right forewing; c, right hindwing; d, apex of hind tarsus, lateral aspect; e, posterior of mesosoma and anterior of metasoma, lateral aspect; f, metasoma, dorsal aspect; g, metasoma and ovipositor, lateral aspect; h, vein 1-SR+M of right forewing; i, vein 1-M of right hindwing. Scale line: a = 0.25 mm; b,c,e,f,g = 2.0 mm; d = 0.5 mm; h,i = 0.1 mm.

Cove, Sydney, NSW; holotype collected 17 July 1943; paratype collected on 11 Aug. 1946.

**Description.** *Females*. Length of body 13.3-13.5 mm, of forewing 11.3-12.5 mm, of ovipositor (part exserted beyond metasomal tergites) 14.5-16.0 mm and of antenna 12.5 mm.

Antenna with 44-45 flagellomeres; approximately as long as the forewing. Terminal flagellomere 2.4 x longer than maximally wide. Penultimate flagellomere 1.6 x longer than wide. Median flagellomeres parallelogram-shaped in profile; 1.7 x longer laterally than wide. First flagellomere 1.17 x and 1.37 x longer than the 2nd and 3rd respectively, the latter being 1.7 x longer than wide. Ratios of height of clypeus : intertentorial distance : tentorio-ocular distance = 16 : 19 : 25. Malar space 0.76 x height of eye. Ratios of height of eye : width of face : width of head = 33 : 57 : 91. Facial ridge with fine longitudinal carinae. Antennal sockets with crenulate margins anteriorly and laterally. Frons with fine curved carinate sculpture. Ratios of distance between posterior ocelli : transverse diameter of posterior ocellus : shortest distance between posterior ocellus and eye = 3 : 2 : 6.

Mesosoma 1.64 x longer than high. Scutellar sulcus with 6 or 7 transverse crenulae. Scutellum sometimes with a short midlongitudinal row of fine pits.

*Forewing*. Ratios of lengths of veins r : 3-SR : SR1 = 4 : 3 : 24. Ratios of lengths of 2-SR : 3 - SR : r-m = 6 : 3 : 5. Vein m-cu 2.5 x longer than shortest distance between 1st discal cell and 2nd submarginal cell. Vein 3-CU1 very weakly expanded posteriorly.

*Hindwing*. Vein M+CU 2.9 x longer than 1-M.

Ratios of lengths of fore femur : tibia : tarsus = 79 : 88 : 105. Fore basitarsus 8.4 x longer than maximally deep. Ratios of lengths of hind femur : tibia : tarsus = 50 : 86 : 68. Hind basitarsus 7.7 x longer than deep. Hind femur 9.5 x longer than deep. Inner hind tibial spur 0.16x length of hind basitarsus.

First metasomal tergite 1.1 x longer than maximally wide, not narrowing behind the basodorsal lobes. Second tergite 2.35 x wider than long.

Antennae, apical 3 segments of both pairs of palps, stemmaticum, tegulae, scutellum, mesopleuron, mesosternum, metanotum, anterior half of propodeum and metapleuron, forelegs (except for coxae), ventral side of femur, mid- and hindlegs, metasomal tergites 2-4, metasomal sternites (except for hypopygium) and ovipositor sheaths, black. Posterior halves of propodeum and metapleuron, first metasomal tergite except for a small dark mark medioposteriorly, ivory white. Remainder of head and body, orange-red. Wing venation piceous brown, wing membrane more or less evenly light brown.

## Discussion

Members of the Helconinae possess many plesiomorphous character states, and the subfamily as whole is difficult to characterise on the basis of apomorphous character states and tends to fall out at the end of keys to braconid subfamilies (van Achterberg, 1976). The presence of a distinct forewing costal cell (Fig.2b), forewing veins 1A and 2A, hindwing vein 2A, complete occipital, hypostomal (Fig.1d) and prepectal carinae (Fig.1e) and having metasoma inserted above the hind coxae collectively indicate an early origin from the remainder of the family. Nevertheless, the Helconinae appears to be clearly associated with the majority of non-cyclostome, braconid subfamilies on the basis of their endoparasitism, of the presence in young larvae of an evaginated rectum (both apparently apomorphous character states) and by the possession of a weakly muscularised, thin walled venom gland reservoir (type II of Edson & Vinson, 1979) (a plesiomorphous character state).

Further, in all of van Achterberg's (1984) groups III (excluding the Betylobraconinae which belong elsewhere) and IV comprising the subfamilies Helconinae (except for *Calohelcon*), Meteorideinae, Blacinae, Euphorinae, Cercobarconinae, Trachypetinae, Xiphozelinae, Homolobinae, Sigalphinae, Cenocoeliinae, Agathidinae, Macrocentrinae, Amicrocentrinae, Orgilinae, Cheloninae, Neoneurinae, Cardiochilinae, Khoikhoiinae and Microgastrinae, hindwing vein m-cu is absent. In contrast, m-cu is present, albeit with a rather reticulate distribution in the Alysiinae, Betylobraconinae, Doryctinae, Gnamptodontinae, Histeromerinae, Opiinae, Rogadinae and Telegaiinae. Clearly, m-cu has been repeatedly lost within the Doryctinae and Rogadinae but it is represented in many distantly related genera in both of these subfamilies. It is never present in the Braconinae although a possible remnant may be present at the base of the poorly developed distal abscissa of the cubital vein (?3-CU) present in some *Calcaribracon* Quicke. It is also absent from the Mesostoinae which show a marked reduction in venation (van Achterberg, 1975).

The presence of a trace of m-cu in *Calohelcon* firstly reinforces the notion that the Helconinae is a group that has diverged relatively little from the ancestral braconid groundplan. Secondly, it raises the problem of whether its presence in *Calohelcon* should be regarded as plesiomorphous or apomorphous. If plesiomorphous, then the assumption is made implicitly that it has been retained in all the ancestors of the taxon under consideration. Thus, considering what we know of the relationship of the Helconinae and the relationships within the Braconidae in general, would appear to be less parsimonious than assuming a re-expression of a gene or genes for vein m-cu is also absent in the Ichneumonidae. Riegel (1948) and Tobias & Belokobylsky (1983) similarly use the occurrence of aberrant wing venation features in the Braconidae as a means of interpreting phylogeny. Forewing vein 2m-cu is a good example. It is present in the vast majority of Ichneumonidae (it is only absent in a few species) but has also been found as an aberrant condition in *Histeromerus* Wesmael (Histeromerinae) and *Orgilus*

Haliday (Orgilinae) and is 're-fixed' in *Apozyx* Mason (a member of the cyclostome group of Braconidae; Sharkey, personal communication). A similar interpretation seems to be appropriate for the presence of hindwing vein m-cu in *Calohelcon* and indeed in the other braconids which possess it. Nevertheless, we do not want to suggest that the reappearance of such 'plesiomorphous' character states is independent of phylogenetic position or of evolutionary distance. Such re-expressions critically depend on the retention within the organism's genome of ancient genetic information (unless one assumes an evolutionary predisposition to re-evolve given 'genes' *de novo*). It is not surprising therefore that hindwing vein m-cu is present in a helconine given that members of this subfamily appear to possess many other plesiomorphous character states.

We should like to point out, however, that current computer programs for finding the most parsimonious cladogram for a group of taxa fail to treat such characters adequately, and care should be taken when considering the significance of phylogenetic decisions based on probable character re-expressions as opposed to truly plesiomorphous states for which there has been a complete evolutionary continuity from the ancestral (root) taxon. The placement of *Apozyx* in a separate family (the Apozygidae Mason, 1978) is a case in point, the presence of a forewing vein 2m-cu having been taken to outweigh all the other characters indicating that *Apozyx* should be regarded as an aberrant cyclostome braconid (Mason, 1978; Sharkey, personal communication).

In addition to the presence of hindwing vein m-cu, several other characters occurring in *Calohelcon* and other Helconinae warrant further discussion and are considered below.

*Lateral carina of mesoscutum.* Van Achterberg (1979a) states that the absence of a lateral mesoscutal carina in his new subfamily, the Amicrocentrinae, should be considered as plesiomorphous. However, a well-developed carina is present in most, if not all Helconinae, and therefore, since this subfamily undoubtedly had an ancient origin, it seems reasonable to consider that the presence of a lateral mesoscutal carina is a plesiomorphous character state for the Braconidae, otherwise it has to be assumed to have arisen independently. Further, it should be noted that many Ichneumonidae have a well-developed (even if somewhat obscured) lateral mesoscutal carinae (e.g. many Pimplinae, Tryphoninae).

*Forewing with an open costal cell.* An open forewing costal cell (Fig.2b) is known to occur in only a few subfamilies of Braconidae, it is best developed in the Amicrocentrinae (van Achterberg 1979a, 1983a) but a partly open cell is also found in some Helconinae and Trachypetinae. It is unknown among the Ichneumonidae. An open costal cell is undoubtedly the plesiomorphous condition for the Hymenoptera as it represents a more complex venational state as seen in the Symphyta and also in the extinct Praeichneumonidae (Rasnitsyn, 1983). Closure of the costal cell is usually considered a synapomorphy for the Braconidae + Ichneumonidae and it should be pointed out that it is highly unlikely that the somewhat open costal cell found in these three braconid subfamilies represents a continuity in evolution from the Symphyta all the way through to the Braconidae; if that were the case then one requires multiple independent closures of the costal cell at least in three lineages of braconid subfamilies and also in the Ichneumonidae. It seems to us more likely that, as argued for hindwing vein m-cu above, an open costal cell represents the re-expression of genes which have previously been suppressed. Thus, strictly speaking, such character re-expressions should be regarded as apomorphous rather than plesiomorphous character states, albeit that they may be more likely to be re-expressed in groups showing a large proportion of other, truly plesiomorphous character states such as in the Helconinae.

*Position of spiracles of second metasomal tergite.* Van Achterberg (1984) regards the plesiomorphous character state for the Braconidae to be with the spiracles located in the tergum as is the case in its sister group, the Ichneumonidae rather than in the latero-tergite (= epipleuron). Care has to be taken when examining this character in some Braconidae, because the lateral crease of the second metasomal tergite does not necessarily coincide with the border between the tergum and the laterotergite (e.g. in the Histeromerinae). However, in *Calohelcon*, KOH treatment of the metasoma reveals a distinct zone of reduced sclerotisation corresponding with the lateral crease of the second metasomal tergite and corresponding zones in the less distinctly creased or uncreased posterior tergites. Thus, in this genus there can be no doubt that the spiracles are located in the true laterotergites (Fig.3g). Given this and the overall assemblage of plesiomorphous character states displayed by the Helconinae, the possibility that the Helconinae display the plesiomorphous character state for the Braconidae should also be considered. The alternative is that migration of the spiracle into the laterotergite has occurred independently in the Braconidae in at least four lineages (van Achterberg, 1984), viz. in the Alysiinae, in the Aphidiinae, in the Ypsistocerinae + Mesostoinae, and in van Achterberg's proposed lineage III + IV which includes the Helconinae and the majority of non 'cyclostome' subfamilies. Since there appears to have been no such trend in the Ichneumonidae and because the second metasomal spiracle is also situated laterally in the Stephaniidae, it would be more parsimonious to consider this to be the plesiomorphous condition. This view was proposed by Mason (1981) who additionally cites the fact that the second and subsequent metasomal spiracles are situated in the laterotergites in the Symphyta, and that in the primitive subfamilies, Xyelidae and Pamphiliidae, the first metasomal spiracle is also in the laterotergite. Assuming that Mason was correct in his polarity decision, then we see that the majority of cyclostome and related subfamilies of

Braconidae are united by an apomorphous migration of the spiracle to the tergum (subfamilies Braconinae, Vaepellinae (nearly - see Quicke, 1987), Telengaiinae, Doryctinae, Rogadinae, Opiinae, Gnamptodontinae, Histeromerinae (the statement in van Achterberg, 1984 is incorrect) and Betylobraconinae (the placement of this subfamily in van Achterberg's, 1984 cladogram is considered erroneous; Tobias, 1979; Sharkey, personal communication). The placement of the remaining subfamily with a notal spiracle van Achterberg's (1984) Dirrhopinae needs further consideration but it appears to be close to the Microgastrinae (Sharkey, personal communication). With this arrangement three reversals only have to be cited; for Alysiinae which has the second spiracle in the epipleuron, in the Dirrhopinae and in the peculiar subfamilies Ypsistocerinae and Mesostoinae. The Ypsistocerinae are associated with termites and may be derived from the Doryctinae. The Mesostoinae are very small wasps and too poorly known for further comment.

*Number of hamules.* The plesiomorphous number of hamules on vein R1 of the hindwing of Braconidae is approximately ten as indicated by outgroups comparison with the Ichneumonidae (Townes, 1969) and other equivalent sized Hymenoptera. However, in the majority of Braconidae, the number is usually reduced to three or sometimes up to six. Few braconids other than *Calohelcon* have eight to ten. Among these are members of the endemic Australian subfamilies, the Cercobarconinae and the Trachypetinae, and it may be significant that *Trachypetus* is one of the few braconids with a partially opening forewing costal cell. Thus, the number of hamules indicates another possibly atavistic character state in *Calohelcon* and in the Trachypetinae.

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# A New Species of *Pteralopex* (Chiroptera: Pteropodidae) from Montane Guadalcanal, Solomon Islands

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ABSTRACT. *Pteralopex pulchra* n.sp. is described. It is known from a single specimen collected at 1,230 m on the south slopes of Mount Makarakomburu, Guadalcanal, Solomon Islands. It is probably restricted to altitudes in excess of 1,200 m, where it possibly replaces *Pteralopex atrata* which is restricted to lower elevations. This species pair possibly forms the only example among Solomon Islands mammals of altitudinal replacement. The morphology of *P. pulchra* n.sp. is intermediate in some respects between that of the two previously known Solomon Islands species (*P. anceps* and *P. atrata*), and the Fijian *P. acrodonta*. *Pteralopex pulchra* n.sp. is unique however in the possession of extensively black and white mottled wings, bright red eyes and a yellowish venter which contrasts strongly with the blackish back.

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The first species of the genus *Pteralopex* to become known was *P. atrata*, described by Thomas (1888) who based his description upon material collected by C.W. Woodford at Aola, Guadalcanal Island, Solomons. These specimens were almost certainly collected near sea level as Woodford (1890) states that he was unable to penetrate far inland during his stay at Aola. In 1909 Anderson described a second and closely related species, *P. anceps* from Bougainville. Sanborn (1931) subsequently reported *P. atrata* from Santa Isabel (also known as Ysabel), while Phillips (1968) recorded *P. anceps* from Choiseul. Figure 1 shows the distribution of these species. The two species were considered to be distinct until Laurie & Hill (1954), then Phillips (1968) treated *P. anceps* as a subspecies of *P. atrata*. In 1978 Hill & Beckon described a third species, *P. acrodonta*, from montane forests on Taveuni, Fiji. They also reconsidered the taxonomic status of the Solomon Island forms, and considered that there were good grounds for the recognition of two distinct species in these islands, *P. atrata* from Guadalcanal and Ysabel, and *P. anceps* from Bougainville and Choiseul.

The new species of *Pteralopex* described here was discovered during a survey of the mammals of the south-west Pacific region organised by the Australian Museum. It is based upon a single individual whose morphology

is so different that I have no doubt as to its distinctness from all previously described forms. I have compared it with a large and previously unreported series of *Pteralopex atrata* and *P. anceps* held in the Australian Museum. All of the seven *P. atrata* in the latter collection are from Guadalcanal, while the *P. anceps* are from Bougainville (6) and Buka Island, north of Bougainville (1).

Hill & Beckon (1978) diagnose the genus *Pteralopex* by its possession of the following features: the wings are inserted at or near the midline of the back along the spine, the sagittal crest is well developed, the postorbital processes usually reach the zygomata, the orbits are upwardly directed, the rostrum is short and parallel sided, the upper canines massive, the I/2 enlarged, and the molariform teeth are cuspidate. They also list a series of more minor dental features. All of these features are characteristic of the new species.

## Materials and Methods

The comparative material used during this study is listed in Appendix 2. Some of the measurements in Table 1 (Appendix 1) were taken from Hill & Beckon (1978). Dental terminology follows Hill & Beckon (1978), except that 'premolar' is abbreviated as 'P' rather

**Fig.1.** Map of the Solomon Islands showing locality records for the species of *Pteralopex*. Dots = *P. anceps*, stars = *P. atrata*, star in circle = *P. pulchra*. The occurrences on Choiseul and Ysabel are not localised beyond the island upon which the specimen was collected.

than 'pm'. The holotypes of the three previously described species of *Pteralopex* were examined and photographed during a visit to the British Museum (Natural History) during November 1989. Colour terminology where capitalised follows Smithe (1974). All measurements are in mm and weights in grams. The holotype of *P. pulchra* was measured and weighed when freshly dead in the field. Summary statistics were generated using the STATISTIX package.

## Systematics

***Pteralopex*** Thomas, 1888

***Pteralopex pulchra* n.sp.**

Figs 2,3, Table 1

**Type material.** HOLOTYPE, AM M21842 (field number LA255), adult female body in spirit, with the tongue, eyes and parts of the masseters retained and the skull cleaned and extracted. Collected on 17 May 1990 in a mistnet set at 1,230 m altitude, southern slopes of Mount Makarakomburu (9°44'S 160°01'E), by T. Flannery, I. Kaujare and T. Leary. Breast muscle was extracted and placed in 90% alcohol in the field, and samples of liver, kidney and heart were frozen in liquid nitrogen.

**Etymology.** Beautiful (L.), the generic name being feminine. For the striking red eyes, black and white wing membranes and yellowish venter which together make this the most attractive of the *Pteralopex* species.

**Diagnosis.** Smallest species of *Pteralopex*, differing in possession of extensive black and white mottling on wings, white ear bases and contrasting dorsum and venter. Further differs from *Pteralopex atrata* and *P. anceps* in narrower ears, yellowish rather than blackish venter, and, except some *P. atrata*, P/3 lacking anterolingual cusp. Further differs from *P. acrodonta* by less cuspidate molars, smaller M2/, M/3, and black dorsum.

**Description.** Holotype weight = 280 gms. Head-body length = 161.8 mm, ear length = 16.8 mm, tibia length = 56.1 mm, hindfoot length = 43.1 mm. Nipples and mammary glands very prominent in life and milk could be extruded. Ears short and narrow, rising to a blunt tip, entirely hidden by fur in life (thus differing markedly from broad, more rounded ears of *P. atrata* and *P. anceps*). Ears with sparse covering of long black hairs both internally and externally. Distalmost three quarters of ear black, but base, both internally and externally, is white. Wings inserted along midline of spine, and posteriorly at base of second toe. Dorsal surface of wing black, ventral surface strikingly patterned black and white. Mottling irregular; white predominating anterior to forearm, in middle portion of wing proportion of black and white approximately equal, while along posterior margin black predominates (Fig.2). Three specimens of *P. atrata* have much more limited white

**Fig.2.** The holotype of *Pteralopex pulchra* in ventral view in life.

mottling. Small claw present on digit 2. Calcar length = 13 mm, interfemoral membrane black and approximately 13 mm wide on each side, joining at posterior end of body to form a narrow flange. Fur of head, face and back is long, woolly and blackish. Venter largely yellowish, close to Buff. Midline of venter has pale Cream line approximately 1 cm wide extending entire length of the body. Fur of venter darkens at posterior of body. Band of long Buff hairs extends along ventral surface of ulna and onto wing membrane for about 20 mm posteriorly. Tibia well furred with black hairs to ankle. Back densely furred in long black hairs, extending onto proximal third of forearm. Iris in life bright red, from memory close to Poppy Red.

Cranium and dentaries (Fig.3) are largely similar to *P. atrata*, but smaller, more gracile. Rostrum relatively narrower; sagittal crest less well developed.

Only single soft palate of *P. atrata* available for comparison; both species with 8 well-defined ridges posterior to P4/. Differs markedly from *P. atrata* in that *P. pulchra* ridges form much tighter arcs and posterior 6 are ornamented with anteriorly-projecting serrations (Fig.3). Similar serrations evident only on posteriormost 2 ridges in *P. atrata*. Anterior part of palate similar in both, but again all 4 ridges form more acute arcs in *P. pulchra*.

Dentition largely similar to *Pteralopex atrata*, but differs in following ways; all teeth smaller, but largely similar proportions. Upper canine differs only in that posterolingual cusp less well developed. P2/ even more rudimentary than *P. atrata*. P3/ differs in having distinct posterobuccal cusp, while P4/ lacks posterobuccal cusp (present in 2 out of 3 *P. atrata* available). I/2 relatively more reduced. P/3 strikingly different; in *P. pulchra* no anterolingual cusp, anterior of tooth dominated by single sharp cusp from which sharp ridge descends anteriorly. A single specimen of *P. atrata* has similar morphology. P/4 differs in that anterior cingulum not as well developed as *P. atrata*. M/1 differs in that

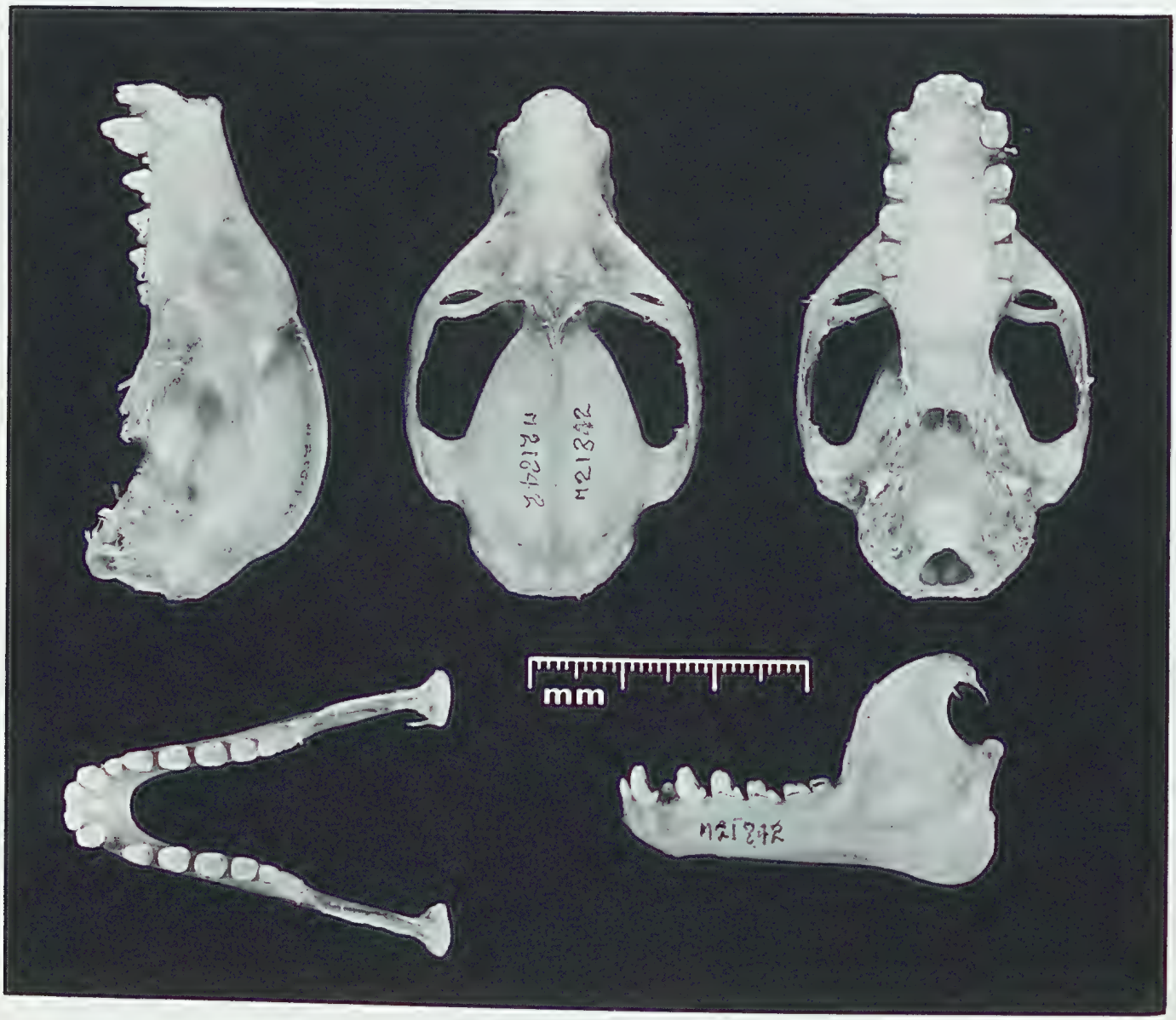


**Fig.3.** The skull and dentaries of AM M21842, the holotype of *Pteralopex pulchra*.

principal anterior cusp not as large, but anterolingual cusp larger, comprising lingual third of anterior part of tooth.

## Discussion

*Pteralopex pulchra* shares similarities with *P. acrodonta* on the one hand, and the two Solomon Island species *P. anceps* and *P. atrata* on the other. It is similar in size to *P. acrodonta*, and both share the distinctive P/3 morphology where the anterior part of the tooth consists of a single cusp and anterior ridge. Similarities shared with the other two Solomon Islands species include reduction of the posterior molars and less cuspidate molars and P4/ (although an additional labial cusp is present on P4/ in *P. pulchra*).

Analysis of the phylogenetic relationships of the species of *Pteralopex* must await a full biochemical and morphological study, which I hope to undertake when sufficient material has been accumulated. However, the P/3 morphology of *P. acrodonta* and *P. pulchra* probably represents something near the plesiomorphic condition, as a similar morphology is seen in the four species of the *Pteropus pselaphon* group, considered by most workers (e.g. Hill & Beckon, 1978) as being closely related to (and thus a good outgroup for) the species of *Pteralopex*.

Little is known of the biology of *Pteralopex pulchra*. The only known specimen, a female, was lactating when caught on 17 May 1990. It was caught in a mistnet set on a cleared ridgetop at 1,230 m elevation on the southern slopes of Mount Makarakomburu. The forest where the net was set was low (canopy height on the ridge around 4 m), although emergent *Metrosideros collina* trees reached 10 to 15 metres. The *Metrosideros* was flowering at the time of the visit. The forest itself was very mossy, with tree-ferns being abundant. Climbing bamboo was a common element, as was a species of *Acmena*. Palms (represented by several species) were also abundant, and in parts the forest floor was littered with fallen palm fruits which were around 1 cm in diameter. A large palm which seemed to be restricted to elevations above 900 m was carrying large bunches of conspicuous red fruit.

The night before capturing the holotype in a mistnet I spotlighted an individual almost certainly representing this species at around 1,200 m. It was seen at around 10.15 pm hanging in a *Metrosidros collina* beside the track. Extensive mistnetting and spotlighting below 1,200 m failed to reveal the species. The highest elevation reached by our survey was 1,230 m. *Pteropus woodfordi*, *Melonycteris* sp., *Nyctimene albiventer* and *Macroglossus minimus* were taken in the same mistnet on the night of the capture.

Upon the basis of mistnetting and spotlighting results I suspect that *Pteralopex pulchra* may not occur below around 1,200 metres. *Pteralopex atrata* occurs at least up to 400 m elevation (AM M19219-20 were taken at this elevation in the Poha River area of northern Guadalcanal), and may well extend higher. However, I saw none during our 1990 survey, which extended from 380 m to 1,230 m on Mount Makarakomburu, southern Guadalcanal, nor, despite intensive effort, was *P. pulchra* seen below 1,200 m. It appears that *P. pulchra* replaces *P. atrata* altitudinally above around 1,200 m on the island.

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## APPENDIX 1

Table 1. A series of measurements for the species of *Pteralopex*, taken from Australian Museum specimens and Hill & Beckon (1978). FA = forearm length, GL = greatest length of skull, CBL = condylobasal length, PL = palate length, ON = orbit-nasal opening length, LW = lachrymal width, IW = interorbital width, PW = postorbital width, OD = orbital diameter, ZB = bizygomatic breadth, BB = braincase breadth, MB = bimastoid breadth, CEW = greatest external width across upper canines, CAW = greatest width across upper canine alveoli, CIW = least internal width across upper canines, PIW = least width across upper fourth premolars, MEW = greatest external width across upper first molars, MAW = greatest width across first upper molar alveoli, UTL = length from upper canine to last upper molar, ML = greatest length of mandibles, LTL = length from lower canine to last lower molar. X = mean, R = range, N = sample size, STD = standard deviation.

| | *atrata* | *anceps* | *acrodonta* | *pulchra* |
|---|---|---|---|---|
| FA X | 141.2 | 161.0 | 118.0 | 117.9 |
| R | 137.6-146.6 | 144.8-169.0 | 116.5-119.5 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 3.23 | 8.50 | 2.12 | – |
| GL X | 67.8 | 74.3 | 58.1 | 55.4 |
| R | 65.8-69.9 | 70.2-79.6 | 57.5-58.6 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 1.58 | 3.70 | 0.42 | – |
| CBL X | 64.5 | 70.8 | 56.7 | 53.3 |
| R | 63.0-66.7 | 67.3-75.7 | 56.4-57.0 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 1.54 | 3.50 | 0.42 | – |
| PL X | 36.4 | 40.0 | 32.0 | 31.5 |
| R | 34.7-38.5 | 37.3-43.1 | 31.8-32.2 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 1.22 | 2.32 | 0.28 | – |
| ON X | 17.7 | 19.2 | 15.4 | 15.7 |
| R | 16.8-19.0 | 17.6-21.7 | 15.0-15.7 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.94 | 1.81 | 0.50 | – |
| LW X | 12.8 | 14.3 | 13.5 | 11.0 |
| R | 11.7-13.3 | 13.4-15.0 | 13.4-13.5 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.57 | 0.55 | 0.07 | – |
| IW X | 8.9 | 10.1 | 9.4 | 8.1 |
| R | 8.4-9.6 | 9.5-10.7 | 9.1-9.7 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.38 | 0.46 | 0.42 | – |
| PW X | 6.6 | 7.3 | 7.6 | 6.6 |
| R | 5.4-7.2 | 6.4-8.0 | 7.2-8.1 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.64 | 0.56 | 0.63 | – |
| OD X | 12.8 | 13.8 | 12.5 | 11.4 |
| R | 11.8-13.4 | 13.6-14.3 | 12.4-12.5 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.57 | 0.25 | 0.07 | – |
| ZB X | 38.7 | 42.0 | 33.8 | 32.2 |
| R | 36.9-39.9 | 39.3-44.3 | 32.5-35.1 | – |
| N | 7 | 5 | 2 | 1 |
| STD | 1.20 | 1.82 | 1.84 | – |
| BB X | 22.9 | 25.1 | 21.8 | 21.2 |
| R | 21.7-23.9 | 24.0-26.3 | 21.5-22.0 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.71 | 0.83 | 0.35 | – |

| | *atrata* | *anceps* | *acrodonta* | *pulchra* |
|---|---|---|---|---|
| MB X | 22.4 | 25.2 | 20.8 | 18.8 |
| R | 21.5-23.7 | 24.5-26.0 | 20.6-20.9 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.76 | 0.52 | 0.21 | – |
| CEW X | 16.9 | 18.3 | 14.4 | 12.8 |
| R | 15.9-17.4 | 17.1-18.8 | 14.2-14.6 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.51 | 0.68 | 0.28 | – |
| CAW X | 15.4 | 16.5 | 13.3 | 12.4 |
| R | 14.4-16.0 | 15.9-17.2 | 13.3 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.55 | 0.46 | – | – |
| CIW X | 8.9 | 9.1 | 8.1 | 7.2 |
| R | 8.1-9.5 | 8.1-10.4 | 8.0-8.3 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.44 | 0.81 | 0.21 | – |
| PIW X | 10.7 | 11.2 | 9.6 | 7.6 |
| R | 10.1-11.3 | 10.3-12.1 | 9.4-9.5 | – |
| N | 7 | 5 | 2 | 1 |
| STD | 0.44 | 0.62 | 0.07 | – |
| MEW X | 20.7 | 22.6 | 16.7 | 15.6 |
| R | 20.0-21.6 | 20.4-24.6 | 16.0-16.3 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.57 | 1.47 | 0.21 | – |
| MAW X | 19.2 | 21.0 | 15.5 | 14.7 |
| R | 18.5-20.0 | 19.3-22.0 | 15.1-15.9 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.63 | 1.17 | 0.57 | – |
| UTL X | 26.0 | 28.2 | 22.0 | 19.8 |
| R | 25.2-27.7 | 26.0-29.7 | 21.9-22.0 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.89 | 1.48 | 0.07 | – |
| ML X | 52.7 | 58.5 | 43.9 | 43.2 |
| R | 50.2-54.5 | 53.9-61.6 | 43.3-44.5 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 1.57 | 3.15 | 0.85 | – |
| LTL X | 27.8 | 31.0 | 24.2 | 22.2 |
| R | 27.3-28.5 | 29.0-32.5 | 24.2 | – |
| N | 7 | 6 | 2 | 1 |
| STD | 0.47 | 1.57 | – | – |

## APPENDIX 2

Specimens of *Pteralopex* held in the Australian Museum that were used in this study for comparison with *P. pulchra*.

*Pteralopex atrata*: AM M3374-5, adult males, and AM M4218-9, adult females entire in spirit, collected at Lavors (almost certainly Lavoro Plantation), western Guadalcanal; AM M3373, adult male, body in spirit, skull extracted, same locality; AM M19219-20, adult female skin and skulls, collected at 400 m altitude, Poha River Valley, western Guadalcanal.

*Pteralopex anceps*: AM M6346, entire female in spirits, collected near Buin, south Bougainville; AM M6282-3, AM M6497 adult male, and AM M6347 and AM M6498 skin and skulls collected at Buin, south Bougainville. AM M19822, adult male skin and skull, collected near Malasang Hamlet, Buka Island.

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# Ballarrinae, a New Subfamily of Harvestmen from the Southern Hemisphere (Arachnida, Opiliones, Neopilionidae)

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ABSTRACT. The family Neopilionidae (superfamily Phalangioidea) is redescribed along with a redescription of the monotypic type genus *Neopilio* and the type species *N. australis* Lawrence. The subfamily Neopilioninae is redefined and contains only *N. australis*. A new subfamily, Ballarrinae, is erected for *Vibone* Kauri (southern Africa) and four new genera: *Ballarra*, *Plesioballarra* and *Arrallaba* (southern Australia), and *Americovibone* (southern South America). Nine new species are described: *Ballarra drosera* (type species), *B. alpina*, *B. cantrelli*, *B. clancyi*, *B. molaris*, and *B. longipalpus*; *Plesioballarra crinis* (type species by monotypy); *Arrallaba spheniscus* (type species by monotypy); and *Americovibone lanfrancoae* (type species by monotypy). The Ballarrinae have highly distinctive pedipalps, characterised by a very long patella, a reflexed tibia and an arcuate tarsus with reduced claw. Australian Ballarrinae possess a distinctive penis carrying a left ventrolateral barbed process and an ovipositor with four spermathecae, rather than two which is the condition in other Ballarrinae and most Phalangioidea. Cladistic analysis is used to explore relationships among Southern Hemisphere non-entapophysate taxa, namely Neopilioninae, Ballarrinae, Megalopsalididae and Enantiobuninae, and their relationship with entapophysate Phalangioidea. Alternate hypotheses concerning relationships are discussed. The significance of characters including pedipalp morphology, distribution of plumose setae and abdominal spiracle structure is also discussed.The Neopilionidae *sensu* Silhavy (1970) is a paraphyletic group. The Neopilionidae, as defined in this paper, may also prove not to be a monophyletic taxon. Male specimens of *Vibone vetusta* should help to resolve this question.

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Independently, while researching Australian and South American Opiliones, we found in collections a curious group of phalangioid harvestmen with highly distinctive pedipalps, characterised by having a very long patella, a reflexed tibia and an arcuate tarsus with reduced claw. This pedipalp is very similar to that in the South African species *Vibone vetusta* which Kauri (1961) described and placed in the family Neopilionidae.

Lawrence (1931) erected a new subfamily, Neopilioninae, within the Phalangiidae for the monotypic *Neopilio* Lawrence from South Africa. Characters for his new subfamily included: ozopores visible from above; endites of coxa II not directed towards each other at an angle but more or less forming a straight line at right angles to the long axis of the body; first segment of chelicera without a ventral process, cutting teeth subequal in size; pedipalp patella and tibia densely clothed with setae; and claw minute.

South American taxa were added when Mello-Leitao (1933) described *Acropiliops ruricola* Mello-Leitao and

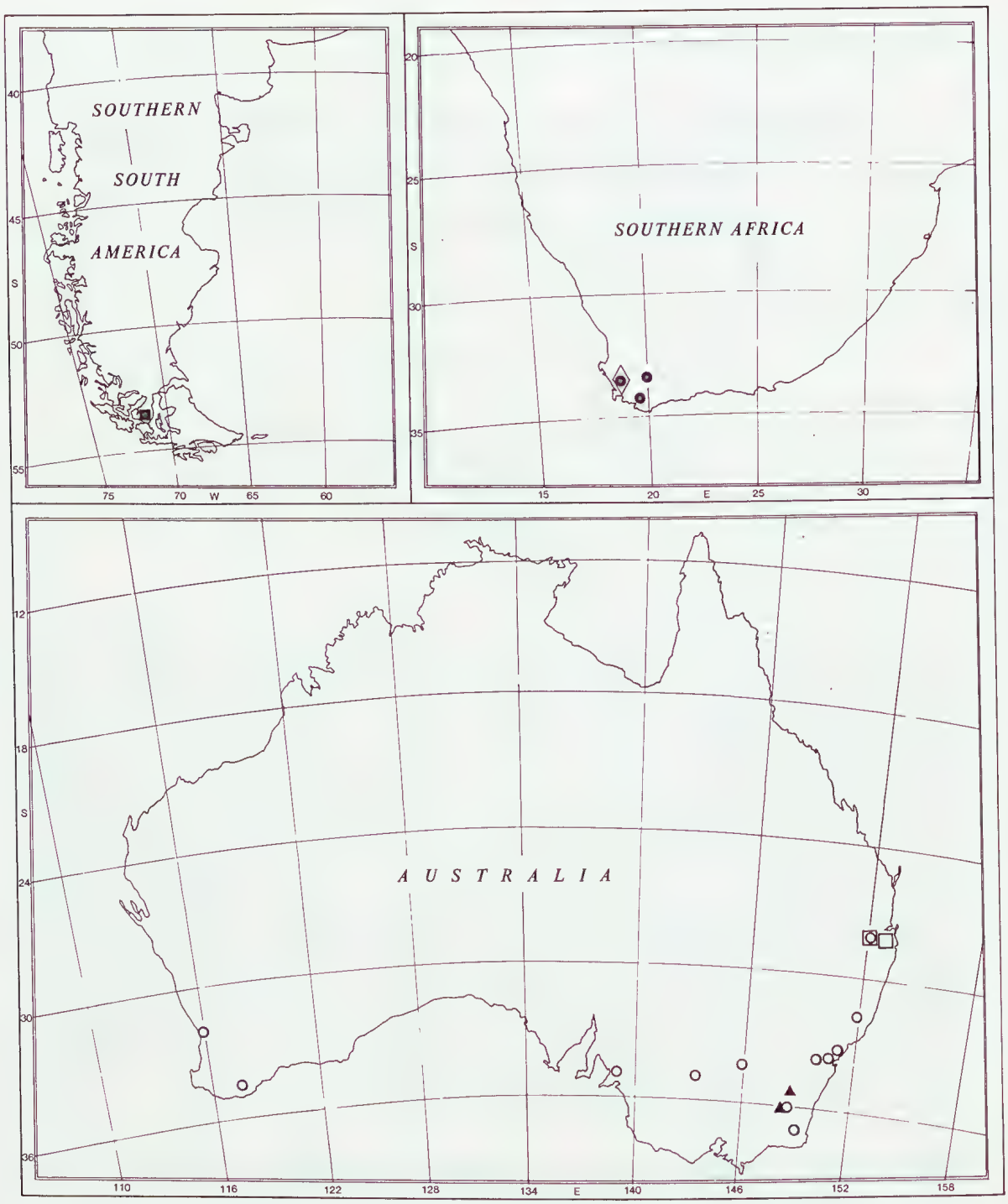


**Fig.1.** Distribution of family Neopilionidae Lawrence. Open circle = *Ballarra*; open square = *Plesioballarra*; closed triangle = *Arrallaba*; closed circle = *Neopilio*; open diamond =*Vibone*; closed square = *Americovibone*.

synonymised the Enantiobuninae with the Neopilioninae. (The Enantiobuninae is recognised by us as comprising *Thrasychirus* Simon and *Thrasychiroides* Soares & Soares; studies of *A. ruricola* reveal it is misplaced in this group and it will be redescribed elsewhere in the Gagrellidae.)

Kauri (1961) added a further genus from South Africa, *Vibone* Kauri, and elevated the Neopilioninae to family rank. Based on his examination of *N. australis*, he believed the abdominal spiracle of the Neopilionidae differed from other phalangioid taxa in lacking an entapophysis and in being occluded by a grill of closely spaced spines. He found that the spiracle of Megalopsalididae lacked both an entapophysis and a grill. Unfortunately, his observation was based on a study of the Western Australian species *Spinicrus minimus* Kauri which has secondarily lost occluding spines and is not representative of the family (Hunt, in press).

Silhavy (1970) reported his light microscopic survey of selected species from each family level taxon in the Phalangioidea. He concluded that Phalangiidae, Sclerosomatidae and Gagrellidae (= Leiobunidae) all have an entapophysis and lack of grill, although some species possess short spines along the posterior margin of the spiracle. The species he examined from Southern Hemisphere taxa, namely the Neopilionidae, Megalopsalididae and Enantiobuninae, all have a spiracle lacking an entapophysis but possessing a grill. On the basis of this character, he united these taxa in the Neopilionidae and recognised three subfamilies: Neopilioninae (southern Africa), Megalopsalidinae (Australia and New Zealand), and Enantiobuninae (South America).

Our studies, and that of Hunt (in press), suggest that the grill can be derived in different ways and is therefore not a synapomorphy linking Southern Hemisphere taxa. Indeed, grill-like structures are illustrated by Starega (1975) for species in the Ischyropsaloidea and Troguloidea. Lack of an entapophysis is a symplesiomorphy. At our present level of knowledge, the Neopilionidae *sensu* Silhavy (1970) is not defined by a synapomorphy and appears to be a paraphyletic group.

Our present paper explores relationships among these Southern Hemisphere taxa with the aid of cladistic analysis. Taxa with the highly distinctive pedipalp are united in a new subfamily, Ballarrinae, and together with *Neopilio*, are placed in a redescribed Neopilionidae.

## Material and Methods

Appendage measurements were done retrolaterally along the dorsal profile, articular membranes excluded. Australian specimens were measured with aid of a camera lucida and Hypad digitiser. Measurements are of the holotype or first listed paratype of the opposite sex unless otherwise stated.

Abbreviations are: BL – body length, CTW – cephalothorax width, CSL – cheliceral second segment length, PFL – pedipalp femur length, LFL – leg II femur length, LTL – leg II tibia length, PL – penis length, ci – character consistency index, ri – character retention index, M – male, F – female, J – juvenile.

The following abbreviations are used to indicate the location of material examined: AM – Australian Museum, Sydney*, ANIC – Australian National Insect Collection, CSIRO, Canberra, FIS – Forschungsinstitut Senckenberg, Frankfurt am Main, JCC – Personal collection J.C. Cokendolpher, Lubbock, MNHN – Museo Nacional de Historia Natural, Santiago, MOV – Museum of Victoria, Melbourne, QM – Queensland Museum, Brisbane, SAMC – South African Museum, Capetown, UQIC – University of Queensland Insect Collection, St Lucia, WAM – Western Australian Museum, Perth. *AM usually denoted simply by the registration number prefix KS.

Cladistic analyses employed Hennig86 Version 1.5 (Farris, 1988) and involved searching for the shortest tree with extended branch swapping (tree-calculating commands mhennig* and bb*). Rooting was initially by the outgroup but resulted in untenable reversals. Rooting was then by a hypothetical ancestor which was plesiomorphic for all characters. The resulting cladograms (Fig.4) appear much more tenable.

## Cladistic Analysis

### Discussion of Characters

Principles summarised by Shear & Gruber (1983) have been used to determine polarity: (1) occurrence in outgroups indicates plesiomorphy, (2) less differentiated, more homonomously patterned characters are plesiomorphic, (3) states resembling those of juveniles are plesiomorphic, (4) characters consistently correlated with others known to be apomorphic are also likely to be apomorphic, and (5) correlations between morphological and ecological or distributional characters should be used cautiously. While principle 2 is not commonly used, others working with Opiliones have found it useful (Shear, 1986; Ubick & Briggs, 1989).

Within the Phalangioidea, family level taxa in the Southern Hemisphere, *viz* Neopilionidae, Megalopsalididae and Enantiobuninae, are all subject to review in evaluating the status of new Australian and South American taxa, namely genera in the Ballarrinae, n. s.fam. Hence, the largely Holarctic entapophysate Phalangioidea was used as an outgroup. The possibility was recognised that this group (consisting of several families) may, in fact, form part of the in-group. For this reason, character states were also polarised by reference to the Caddoidea, the immediate sister group to the Phalangioidea, and the Ischyropsaloidea, the sister group of Phalangioidea + Caddoidea (Martens, 1986).

In the following discussion, numbering of the 20 characters is the same as in Table 1 (see Appendix 1)

and the cladograms (Fig.4). Characters apply to both sexes unless otherwise stated.

**Palpal characters.** A patella longer than tibia (*character 1*) is apomorphic by principal 1. This character appears subject to homoplasy. It was used in the initial analysis, deleted, and the analysis rerun.

A tibia reflexed on the patella so that the dorsal angle between them is less than 180° (*character 2*), together with the lengthening of the patella, is a key synapomorphy of the Ballarrinae which functionally seems to alter the working angle and distance of the tarsus as a raptorial, prey catching organ. A dorsal angle greater than 180° is plesiomorphic by principles 1 & 2.

An arcuate tarsus which is concave dorsad from end to end (*character 3*) is also synapomorphic for these taxa (excluding *Plesioballarra*) though curiously the male specimen of *Americovibone* has a tarsus curved in the opposite sense. The condition in the outgroups where the tarsus is not uniformly curved is plesiomorphic.

A tarsal claw with one or more ventral teeth (*character 4*) is apomorphic; the plesiomorphic condition of no teeth is present in one of the outgroups (Phalangiinae of the Phalangiidae) and in the Caddoidea, the sister group to the Phalangioidea. A process of secondary reduction of teeth is evident in *Pantopsalis* spp. and certain undescribed Australian Megalopsalididae. In New Zealand Monoscutinae (Megalopsalididae), only two teeth are present in *Monoscutum* Forster while they are lacking in *Acihasta* Forster. It is assumed that the single tooth in the Ballarrinae has been derived through loss.

Loss of the tarsal claw or, if present, reduced and reflexed (*character 17*) is apomorphic (principle 1). The reflexed nature of the claw may be correlated with its reduction in *Neopilio* and the Ballarrinae. Character 17 was included in the initial analysis despite being homoplasious as it was a key character for the Neopilioninae *sensu* Kauri (1961). It was deleted from the data matrix and the analysis rerun.

We support Shear's (1986) view that the presence of plumose setae (*character 5*) is plesiomorphic. They are widespread in the Phalangioidea, Caddoidea and Ischyropsaloidea (principal 1) and are present in early nymphal instars in at least *Ballarra clancyi*, n.sp. (principal 3). Absence in the outgroups (and in males of the megalopsalidid *Spinicrus*) is apomorphic. Individual plumes with bifurcating terminations are regarded as plesiomorphic as they predominate and are also present in the Caddoidea, the sister group of Phalangioidea. Plumes with simple terminations are apomorphic but have been excluded from the final analysis because they appear to arise independently in different taxa (*Neopilio*, *Americovibone*, n.sp., and some Enantiobuninae); inclusion creates many additional equally parsimonious trees without clarifying relationships.

*Character 6* in the apomorphic state involves restriction of non-plumose sensory setae and non-socketed setae (or loss of the latter) to the distal tip of the tarsus, together with a correlated distribution of plumose setae along most or all of the tarsus. Functionally, this increases the cover of plumose setae, each of which carries a secretory globule which is thought to assist in food capture. In the plesiomorphic condition (principles 1 & 2), the sensory and non-socketed setae extend along most or all of the tarsus whereas plumose setae are excluded from the distal half. *Plesioballarra*, n.gen., possesses a larger terminal tuft of sensory setae than in other Ballarrinae and plumose setae are excluded from a larger area, the distal 20% (in a New Zealand megalopsalidid from Broken Hut Cave, Te Kuiti, plumose setae extend well into the distal half, being excluded from the distal 30% of the tarsus - this is considered an independently derived condition; non-socketed setae occur profusely along the tarsal length).

Excluding *Vibone* where full data are not available, Phalangioidea with the apomorphic palp configuration (*character 2*) are also apomorphic for characters 3, 5 & 6 suggesting there is a functionally related complex. Treating them as separate characters, as has been done in this analysis, will tend to weight the data set. The *Plesioballarra* palp is of interest because the apomorphic state of character 2, while present, is less fully expressed than in related genera and characters 3, 5 & 7 also tend to be more plesiomorphic.

**Chelicera.** Presence of a ventral process or spur is plesiomorphic by principle 1, its loss is apomorphic (*character 7*). This character appears much subject to homoplasy.

**Legs.** Presence of pseudoarticulations, often manifested as slight swellings or nodules, in at least the femur of leg II (*character 8*) is apomorphic. The plesiomorphic condition is present in the 'Phalangiidae' outgroup, Megalopsalididae, *Neopilio* and some Australian Ballarrinae. The character was included in the initial analysis despite being homoplasious, but was deleted and the analysis rerun.

The presence of teeth on the leg claws of *Americovibone*, n.gen., (*character 18*) is apomorphic by principal 1.

**Penis.** Sclerotised spines or bristles which are associated with the shaft-glans articulation, tend to have side branches or barbs, and usually arise ventrally are known only in three Southern Hemisphere taxa, namely the Megalopsalididae, Enantiobuninae and Ballarrinae. The tendency of cells adjacent to the articulation to lay down such processes was, in preliminary analyses, regarded by us as a synapomorphy at a lower level of universality than the superfamily, even though the processes have three distinct character states diagnostic of the three taxa: Megalopsalididae possess bristle groups, typically two pairs; Enantiobuninae possess single processes, typically two pairs; Ballarrinae possess a single left lateral process which presumably was primitively paired.

Spines or bristle groups are widespread in other

superfamilies including the Caddoidea and Ischyropsaloidea (Martens, 1986) but in the Phalangioidea these become largely confined to the shaft-glans articulation, or are lost. Hence, in our final analyses, we have regarded the position of these processes as a synapomorphy at the level of the Phalangioidea, that is a plesiomorphy at the family level. Loss of the processes is apomorphic (*character 9*).

The condition in Enantiobuninae most closely resembles that in the Caddoidea and hence is regarded as more plesiomorphic. The bristle groups of the Megalopsalididae (*character 10*) and the single barbed process in the Ballarrinae (*character 11*) are apomorphic.

Nevertheless, the three types of processes associated with the shaft-glans articulation may be interpreted in at least two other ways: as autapomorphies derived from a plesiomorphous naked state, or as autapomorphies derived from a plesiomorphous state of numerous ungrouped spines.

A greatly enlarged barbed process (*character 19*) is autapomorphic for *Arrallaba*, n.gen.

An elongate stylus (*character 12*), present in most Ballarrinae, is regarded as apomorphic by principle 1.

The relative lengths of the penis muscle and its tendon show interesting variation tending to fall into two basic character states: long muscle with short tendon, and short muscle and long tendon (Fig.2). The latter is considered apomorphic but the character is not used in the analysis as it appears to have arisen independently in several taxa.

**Ovipositor.** Although there has been debate as to whether two or four seminal receptacles (*character 13*) is apomorphic for the Phalangioidea (Shear, 1986), we regard two as apomorphic and four as plesiomorphic. Four occur only in the Ballarrinae, in New Zealand Monoscutinae and a possibly related new genus in Australia, and in some *Pantopsalis* spp. (Forster, 1964). In every species examined the dorsal-ventral pair is reduced (Fig.3), extreme reduction occurring in the

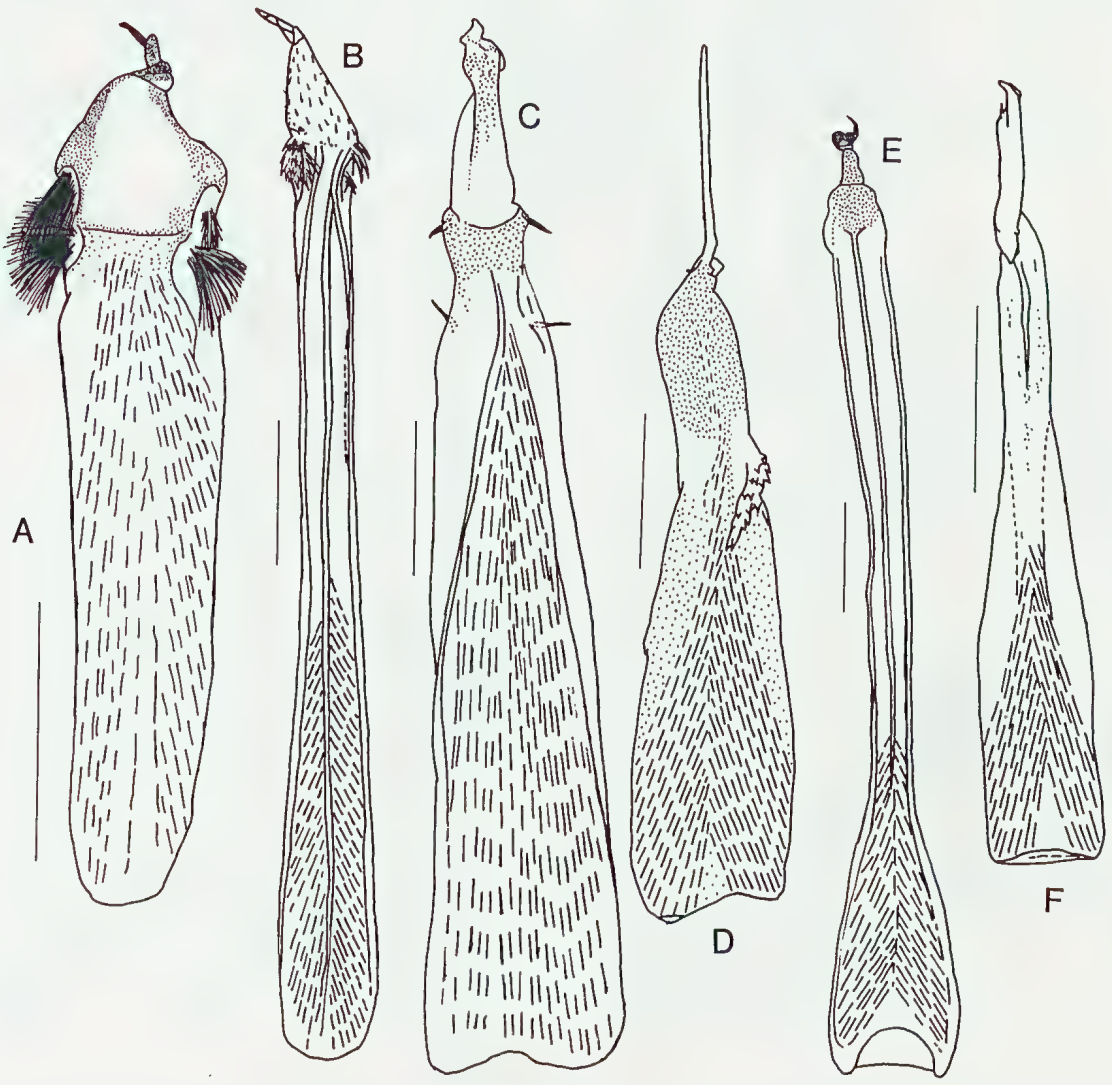


**Fig.2.** Penis variation in non-entapophysate Phalangioidea. A. Megalopsalidinae (*Spinicrus* sp. *ex* Sydney); B. Monoscutinae (*Acihasta salebrosa* Forster); C. Enantiobuninae (*Thrasychirus* sp. *ex* Osorno, Chile); D. Ballarrinae (*Ballarra alpina* n.sp.); E. Neopilioninae (*Neopilio australis* Lawrence); F. Ballarrinae (*Americovibone lanfrancoae* n.sp.). F, dorsal; others ventral. Scale bars 0.1 mm.

monoscutine *Acihasta salebrosa* Forster. In those Megalopsalididae with two receptacles it is the lateral pair that is present. The analyses, however, tend to treat this character as a reversal.

The presence of sensory lobes carrying sensory tufts is plesiomorphic (principal 1). The absence or reduction of the lobes with retention of the sensory tufts is a synapomorphy for the Enantiobuninae (*character 14*).

The presence of only two segments in the ovipositor corpus of *Vibone* (*character 20*) is apomorphic (principal 1). Multiple segments are plesiomorphic.

**Spiracle.** A spiracle without an entapophysis was regarded by Silhavy (1970) as a key character uniting several taxa into his expanded Neopilionidae. This character is regarded by us as a symplesiomorphy (principles 1 and 2). The apomorphic state of *character 16* is a spiracle with an entapophysis and attached muscle which serves to vary the spiracle aperture. It may or may not have grill-like occluding spines. Functionally, the entapophysis with its associated muscle closes the spiracle, presumably limiting water loss and entry by parasites. The grill in non-entapophysate taxa forms a baffle which achieves a similar function, though perhaps less efficiently. (It is not known how the peculiar grill structure of *Caddella africana* (Lawrence) (Kauri, 1961: fig.77G) has been derived and whether it is representative of the Caddoidea).

The spines which form the grill (*character 15*) can vary considerably but fall into two basic groups (Hunt, in press): those derived by elongation and branching of simple surface micro-ornamentation (plesiomorphic), or those in the Megalopsalidinae which are derived from more specialised 'lace tubercles' (apomorphic by principles 1 and 2). Although unequivocal lace tubercles have not been seen in the three *Pantopsalis* spp.

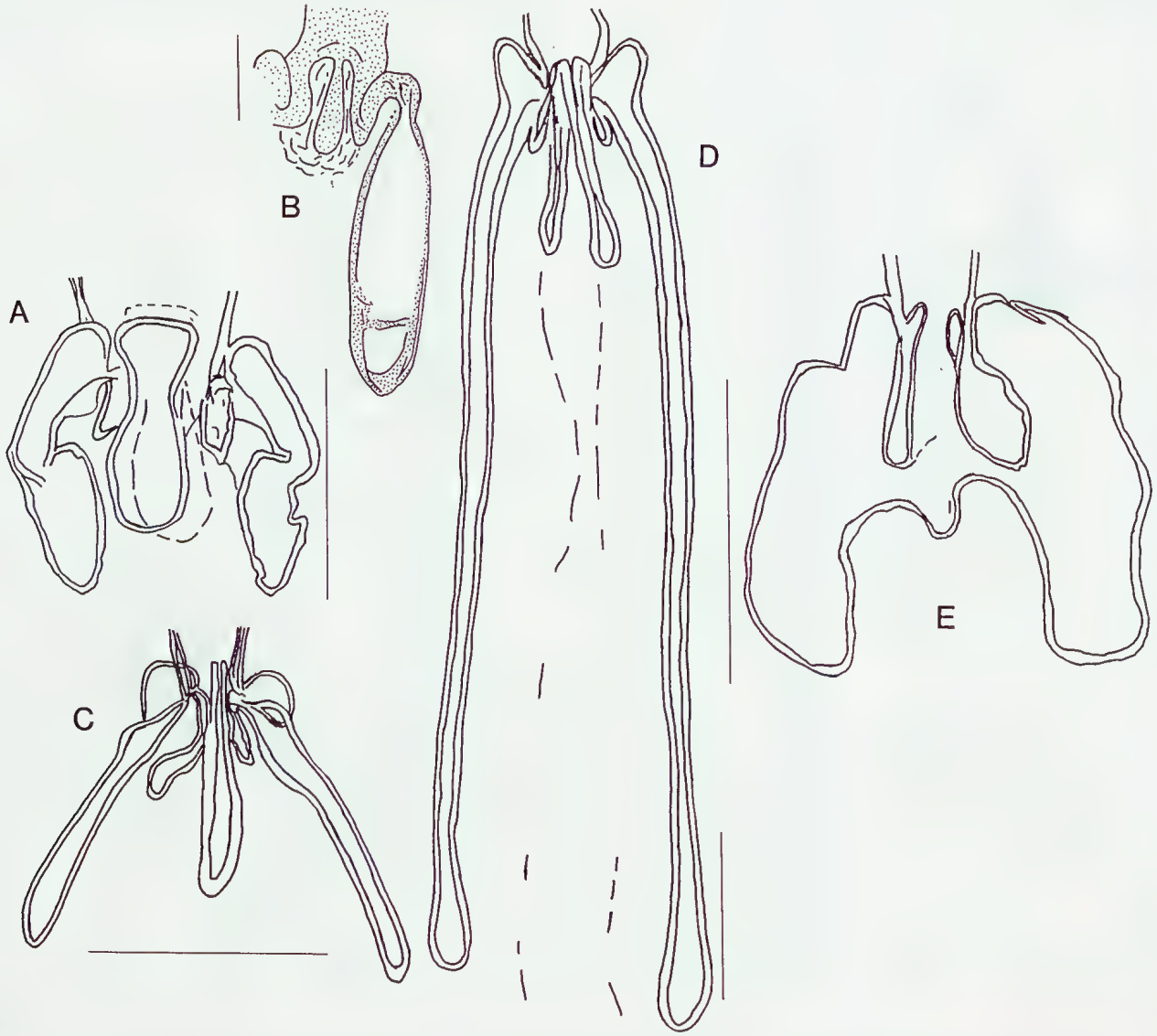


**Fig.3.** Seminal receptacle variation in Megalopsalididae and Ballarrinae. A,B,E Megalopsalididae. A. ?Monoscutinae (new Australian genus); B. Monoscutinae (*Acihasta salebrosa* Forster); E. Megalopsalidinae (*Spinicrus nigricans* Hickman). C,D Ballarrinae. C. *Arrallaba spheniscus* n.sp.; D. *Ballarra molaris* n.sp. Scale bars: B = 0.2 mm; others = 0.1 mm.

examined, lace-like reticulations occur near or on spine bases resembling a condition in Australian Megalopsalidinae (Hunt, in press). Similar reticulations occur on spines in the enantiobunine *Thrasychirus gulosus* Simon and less clearly in *T. dentichelis* Simon, indicating possible homology with the megalopsalidine spines. This latter condition, however, has been coded as 'unknown' in the analysis because of doubts about homology.

The spines in *Neopilio* and Ballarrinae are very similar but appear to be symplesiomorphic.

## Discussion of Relationships

The new subfamily Ballarrinae proved extremely difficult to place within the existing family structure of the Phalangioidea. Several, not necessarily mutually exclusive, hypotheses were evaluated with the help of cladistic analysis. In all analyses, the Ballarrinae were resolved as a monophyletic group, though the possibility of polyphyly is also discussed below.

**Hypothesis 1. The Ballarrinae belongs in the Neopilionidae.** Analyses 1 and 2 support Kauri's (1961) view that *Vibone* is close to *Neopilio* (Fig.4A). Hypothesised synapomorphies are a patella longer than tibia (character 1), and a reduced or lost claw (character 17). Other characters that Kauri regarded as significant in defining the Neopilionidae, *viz* orientation of the endite of coxa II and a non-entapophysate spiracle, are regarded as symplesiomorphous, as are the types of spines forming the spiracle grill.

**Hypothesis 2. The Ballarrinae, Megalopsalididae and Enantiobuninae are monophyletic.** This was supported in analysis 3 where the three taxa were united by a synapomorphy in character 4. The relationship with *Neopilio* + Phalangiidae + Gagrellidae was unresolved because of lack of a synapomorphy. The monophyly of Ballarrinae + Megalopsalididae + Enantiobunidae would be reinforced if our original polarising of character 9 were in error (that is, if the sclerotised processes associated with the shaft-glans articulation are manifestations of a synapomorphy rather than of a symplesiomorphy).

**Hypothesis 3. The Ballarrinae is the sister group of the Enantiobuninae.** If characters 1, 8 and 17 (suspected homoplasies) are excluded (analysis 3), the

**Fig.4.** Cladograms of selected phalangioid taxa. A. Analysis 2, one of 8 shortest trees, length 29, ci 65, ri 77; B. Analysis 3, one of 4 shortest trees, length 24, ci 70, ri 79. Solid bar = apomorphy; solid triangle above = homoplasy; solid triangle below = reversal.

Ballarrinae becomes the sister group of the Enantiobuninae (Fig.4B), though there is a lack of a good synapomorphy (they are united only by a possible synapomorphy in character 7, but we have opted for the choice of this character operating at a different level in the cladogram).

However, in the analyses, it was assumed that the plesiomorphic condition of character 10 (paired single sclerotised processes associated with the shaft-glans articulation) occurred in the Enantiobuninae. This character state may be apomorphic with respect to the bristle groups of the Megalopsalididae, and the unpaired single barbed process in Australian Ballarrinae may be derived from it. Certainly, processes in some Enantiobuninae are barbed and not unlike miniature versions of the ballarrine process. Hypothesis 3 would be supported should these processes prove synapomorphous.

**Hypothesis 4. The Ballarrinae are the sister group of the Megalopsalididae.** Reasons were advanced above for the plesiomorphic status of 4 seminal receptacles (character 13) even though this condition is uncommon in the Phalangioidea. Analysis 3, however, treats them as homoplasic reversals occurring in Australian Ballarrinae and a clade comprising a new genus (?Monoscutinae) and some nominal *Pantopsalis* spp. The former two taxa 'share' another peculiarity: they have sclerotised processes on only one side of the penis though presumably these were primitively paired. However, the ballarrine penis retains the *left* ventrolateral barbed process (character 11) whereas the new megalopsalidid retains its *right* ventrolateral bristles. Nevertheless, the possibility that the ballarrine condition is derived from the other character state through torsion, reduction in number of bristles and enlargement of a single remaining barbed bristle cannot be excluded as these types of developmental processes are involved in penis organogenesis in these groups. Hypothesis 4 would be supported if character 13 proved to be synapomorphous and characters 11 and 20 synapomorphous homologues. Bristles in at least some Megalopsalididae are barbed.

None of the trees in the present analyses showed the Megalopsalididae as the sister group of the Ballarrinae.

**Hypothesis 5. The Ballarrinae should be elevated to family rank.** On the basis of pedipalp structure, the Ballarrinae appear to be a monophyletic group restricted to Gondwanan continental fragments. Synapomorphies uniting the Ballarrinae with *Neopilio* (characters 1 and 17) are subject to homoplasy within the Phalangioidea and are viewed by us with suspicion. Differences separating the Ballarrinae from the Megalopsalididae or Enantiobuninae seem just as marked as those separating entapophysate family taxa.

**Hypothesis 6. The Ballarrinae are a polyphyletic group displaying remarkable convergence in pedipalp structure.** The structure of the ballarrine pedipalp could have originated convergently in one or all of the southern continents as a specialised feeding organ. The fact that nothing closely comparable has been found amongst the diversity of Holarctic or tropical Phalangioidea argues against this hypothesis. Differences in penis and ovipositor morphology between Australian and South American species may argue for it.

## Conclusion

We consider that sufficient evidence will be gathered to support Hypothesis 5. This evidence will hinge on the discovery of the male of *Vibone vetusta* and comparison of its genitalia with other Ballarrinae and with *Neopilio australis*. Insights should arise if the group is found in New Zealand and radiations exist for study in South America and southern Africa.

At present we are retaining this group in the Neopilionidae (Hypothesis 1) on the grounds of nomenclatural stability.

We also believe that the Enantiobuninae, which some analyses gave as the sister group of the Ballarrinae, should be elevated to family rank on the basis of the highly derived form of the glans, and the loss of sensory lobes from the ovipositor (character 14).

The discovery of further characters may help to resolve family level relationships in the Phalangioidea.

## Neopilionidae Lawrence

Phalangiidae: Neopilioninae Lawrence, 1931: 473.–Roewer, 1957: 354.–Ringuelet, 1959: 211.

Neopilionidae: Kauri, 1961: 141-147.–Silhavy, 1970: 171.–Shear, 1975: 68.–Shear, 1982: 110.–Martens, 1978: 55, 229.–Martens, 1986: 304.

**Diagnosis.** Body less than 3.5 mm long. Openings of ozopores visible from above. Endites of coxae II more or less perpendicular to long axis of body. Lateral abdominal sclerites absent. Corona analis absent or vestigial. Abdominal spiracle lacking an entapophysis, occluded by spines arising predominantly from the anterior margin, lace tubercles or spines with lace-like reticulations absent. Penis with one muscle; glans in more or less same axis as shaft; tufts of bristles or paired spines lacking at shaft-glans articulation but left ventrolateral barbed process may be present. Ovipositor segmented; furca 3-segmented and with sensory lobes; 2 or 4 seminal receptacles. Both pedipalp patella and tarsus longer than tibia; femur through tarsus with plumose setae; tarsal claw small or lacking. Chelicerae usually small. Sexual dimorphism usually slight.

**Description**. Body small to medium, usually greater than 0.8 and less than 3.5 mm long. Integument usually thin, at the most with minute spines. Eye mound low, rounded, canaliculate, unarmed or with minute spines. Openings of ozopores visible from above. Last 2-4 abdominal tergites faintly defined by grooves; sternites may or may not be clearly defined. Coxae unarmed ventrally except for small setae; endites of coxae II more or less perpendicular to long axis of body. Lateral abdominal sclerites absent. Abdominal spiracle oval, visible or concealed beneath coxae IV, lacking an entapophysis, occluded by spines arising predominantly from its anterior margin, lace tubercles or lace-like reticulations on spines lacking. Leg tibiae with accessory spiracles, often inconspicuous. Penis with one muscle, muscle long (tendon short) or short (tendon long); glans in more or less same axis as shaft; tufts of bristles or paired spines lacking at shaft-glans articulation but shaft may have left ventrolateral barbed process. Ovipositor segmented; furca usually long and slender, 3-segmented, with sensory lobes; 2 or 4 seminal receptacles. Both pedipalp patella and tarsus longer than tibia, patella often longer than tarsus; femur through tarsus with plumose setae; patella and tibia with or without dense pile of setae; tarsal claw lacking or minute with no ventral teeth, or minute with 1 ventral tooth. Chelicerae small in most species; first segment with or without a ventral spur; jaws with continuous row of teeth of subequal size in most species. Legs long and usually slender; pseudoarticulations often present in all metatarsi, femur II, and tibia II; tarsi each with a simple claw which might have small teeth on each side. Sexual dimorphism slight in most species.

**Subordinate taxa.** Neopilioninae Lawrence, Ballarrinae n.subfam.

## Key to Subfamilies of Neopilionidae

1. Pedipalp patella and tibia with dense pile of setae, dorsal angle between them greater than 180°, plumose setae lacking in distal half of tarsus, patella less than 15% longer than tibia ..... Neopilioninae

—— Patella and tibia lacking dense pile of setae, dorsal angle between them less than 180°, plumose setae present in distal half of tarsus ..... Ballarrinae

### Neopilioninae Lawrence

Neopilioninae Lawrence, 1931: 473.–Roewer, 1957: 354.–Ringuelet, 1959: 211.

**Diagnosis.** Pedipalp patella and tibia thickened and with dense pile of plumose setae; patella only slightly longer than tibia, angle between them greater than 180°; plumose setae lacking in distal half on tarsus; claw without teeth; leg femora and tibiae without pseudoarticulations.

**Description.** Integument very thin and soft. Posterior abdominal tergites and sternites faintly defined by grooves; abdominal spiracle usually not concealed beneath coxae IV; spiracle on leg readily visible. Muscle of penis short (tendon long); shaft without left ventrolateral barbed process. Ovipositor with 2 seminal receptacles. Pedipalp patella and tibia thickened and with dense pile of plumose setae; patella only slightly longer than tibia and angle between them greater than 180°; patella shorter than tarsus, plumose setae lacking on distal half of tarsus; claw inserted terminally, reflexed, without teeth. Chelicerae small, first segment without a ventral spur; jaws each with continuous row of teeth of subequal size. Legs without pseudoarticulations in femora or tibiae, tarsi each with a smooth simple claw. Sexual dimorphism slight, present in pedipalp.

**Subordinate taxon.** *Neopilio* Lawrence.

### *Neopilio* Lawrence

*Neopilio* Lawrence, 1931: 473.–Roewer, 1957: 354.–Silhavy, 1970: 174–Kauri, 1961: 143, 190.–Shear, 1982: 110.

**Type species.** *Neopilio australis* Lawrence, 1931, by monotypy.

**Diagnosis and description.** As for the subfamily.

**Distribution.** Known only from the western Cape Province, Republic of South Africa (Fig.1).

## *Neopilio australis* Lawrence

Figs 5, 6A-D

*Neopilio australis* Lawrence, 1931: 473-474, fig.67.–Roewer, 1957: 354.–Kauri, 1961: 141, 143-145, 185, figs 82, 83.–Silhavy, 1970: 171.

**Type material.** In his description, Lawrence (1931) did not designate a holotype but did refer to 17 specimens from Signal Hill, Cape Town as "Types". This becomes the type series under ICZN Article 72A(b)(vi); 49 other specimens listed are excluded from the type series. In the material examined by us, labels designate two specimens in SAM as "Type No. 1" and "Type No. 2" and 9 specimens in FIS as "Paratypes". LECTOTYPE FEMALE (here designated). Republic of South Africa: Capetown, Signal Hill (Type locality). Label data: "Type No. 1, Signal Hill, from 150,339", coll. Purcell, no other data, SAM. PARALECTOTYPES (here designated). Signal Hill, label data "Type No. 2, Signal Hill, from 150,339", coll. Purcell, 1F, SAM. Signal Hill, "Paratypes", Roewer coll. -Lfd. No. 2937, 3M, 4F, 2J, FIS. An additional 6 specimens in the type series (not examined) are also Paralectotypes.

**Other material examined** (all SAM). Republic of South Africa. Signal Hill: 150,339, Purcell, 7/98, 5F, 7J. 144,02 Purcell, 7/96, 1F. 144,07, Purcell, 9/96, 1F. 150,131, Purcell, 8/01, 1F. 150,130, Purcell, 1F. 150,142, R.M. Lightfoot, 4F. 150,393, Purcell, 8/98, 1M, 2F. 150,338, Purcell, 7/98, 2M. 150,392, Lightfoot, 3/96, 2F. Simonstown: 143,98,

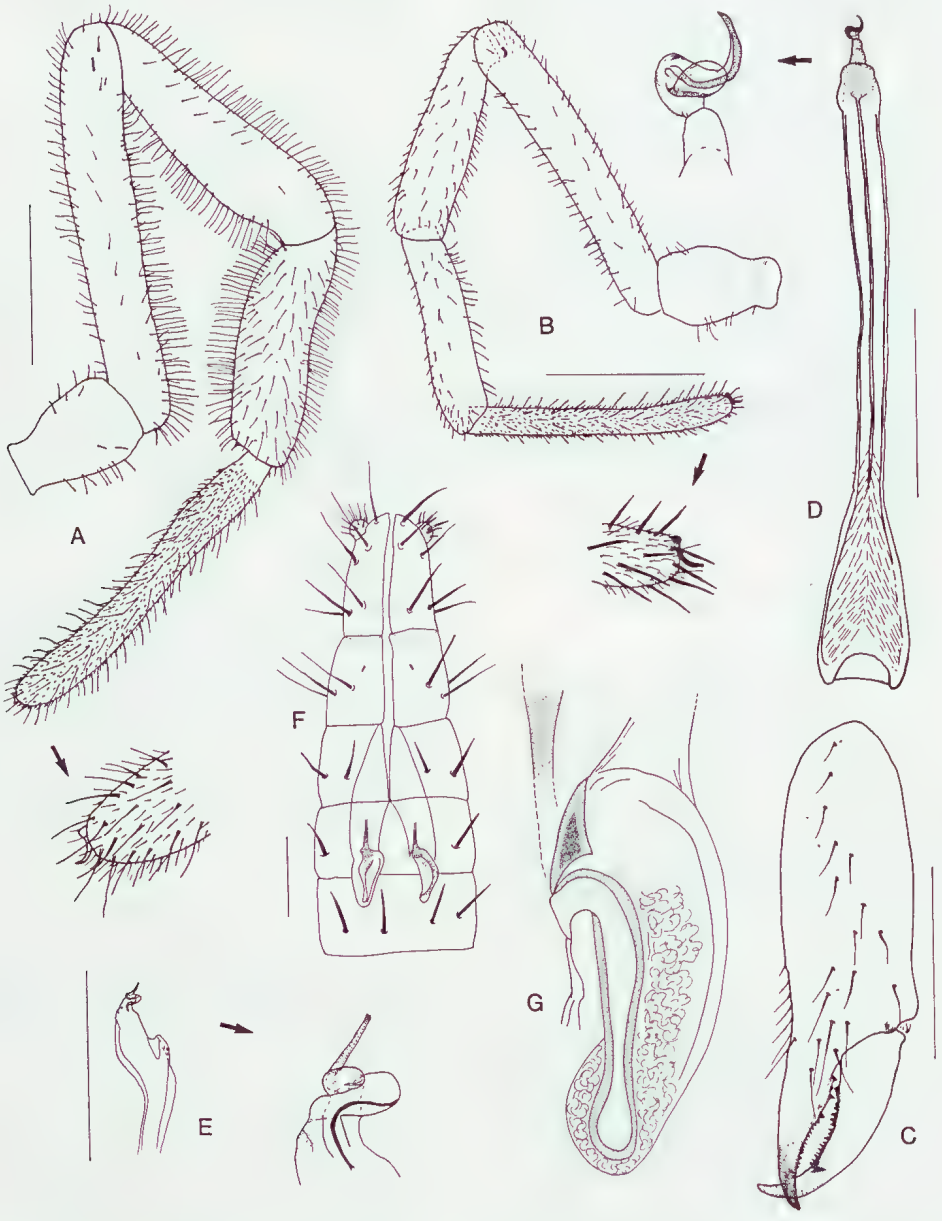


**Fig.5.** *Neopilio australis* Lawrence. A,B. Pedipalp, male & female; C. Male chelicera; D. Penis, ventral. E. Distal part of penis, lateral; F. Ovipositor, dorsal, distal part; G. Detail of seminal receptacle. Scale bars: F = 0.1 mm; others = 0.5 mm.

Prucell, 9/99, 1M. Touws River: 144,00, Purcell, 9/96, 1F. Newlands, Cape Penninsula: 144,10 Purcell, 8/00, 2M. Hout Bay, Cape Penninsula: 150,391, Lightfoot, 2M, 1F.

**Diagnosis.** As for the subfamily.

**Redescription. Males.** *Body.* BL 2.75, maximum width 1.19. Specimens faded; dorsum (at least in females) with faint indication of stripe (Lawrence, 1931: fig.67b), venter pale yellow. Eyes concolorous with body. Anterior margin of cephalothorax smooth, eyemound low, rounded and smooth or with few minute spicules above. Abdominal tergites with a few minute setae, otherwise smooth; coxae and sternites smooth, the former with a few setae.

*Spiracle.* Oval, though posterior margin straighter than anterior; surrounded by a raised annulus, particularly posteriorly; partly occluded by grill of closely spaced branching spines arising from the anterior margin; spines long in some specimens, short in others. Integument anterior and posterior to spiracle with numerous rows of micro-ornamentation, sharp close to the spiracle but more distant microtubercles tend to have expanded,

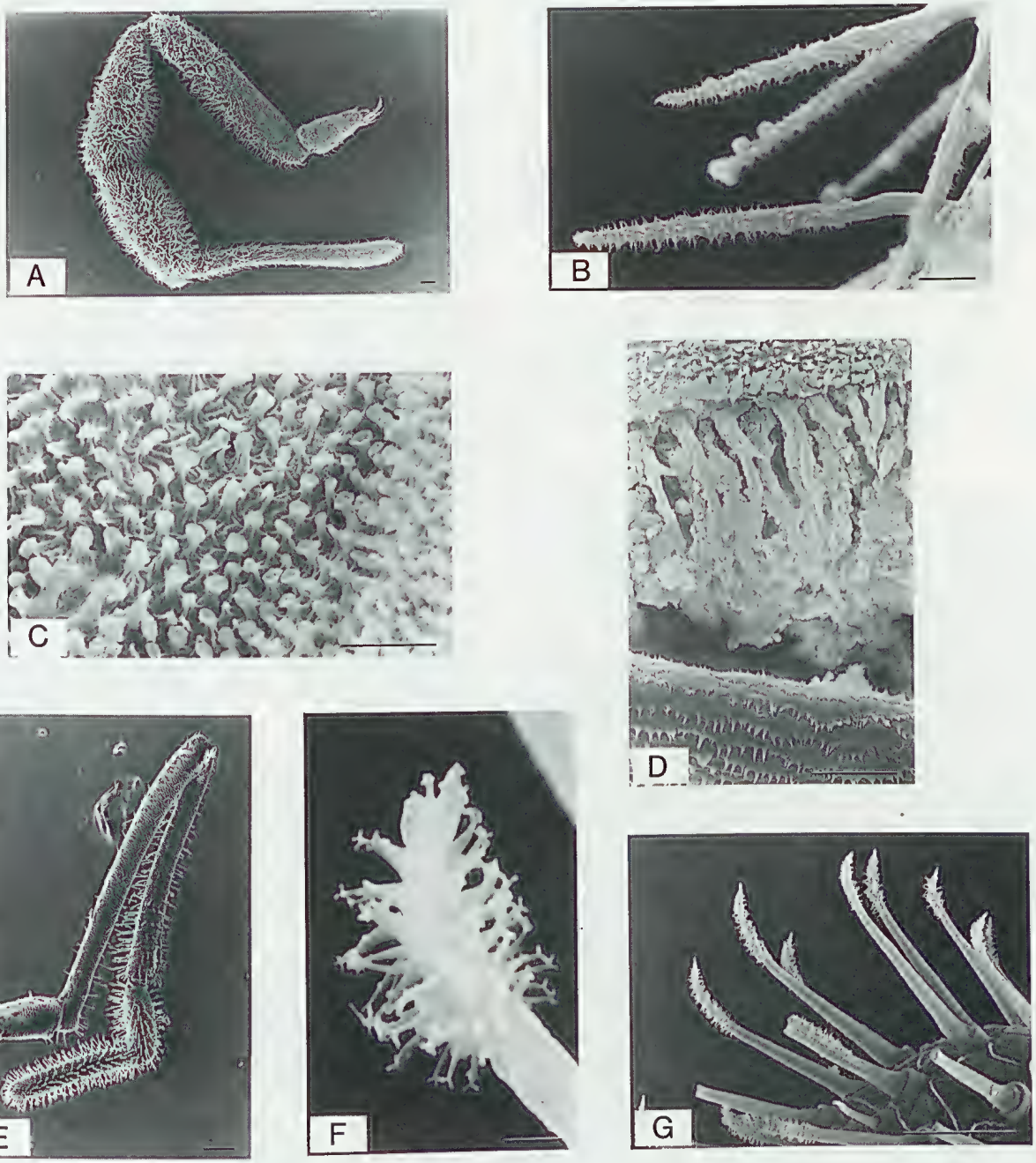


**Fig.6.** A-D. *Neopilio australis* Lawrence. A. Male pedipalp, retrolateral; B. Plumose setae on pedipalp tibia; C. Microsculpture of ventral abdominal integument; D. Detail of spiracle spines. E-G. *Ballarra drosera* n.sp. E. Pedipalp, retrolateral; F. Plumose seta, distal tip; G. Plumose setae on pedipalp tibia. Scale bars: A,E = 100 µm; B-D = 10 µm; F = 1 µm; G = 20 µm.

concave terminations (may be a shrinkage artifact due to very thin integument).

*Chelicerae*. Small, entirely smooth, second segment with small equal-sized teeth in single row, those of the immovable jaw bifid or trifid in proximal half, conical in distal half.

*Pedipalps*. Pale yellow, denticles and claw dark brown. Femur with colourless short setae, more so ventrally; patella, tibia and proximal end of tarsus with brush-like covering; these setae have short plumes along most of their lengths, plumes without terminal bifurcation. Distal half of tarsus with sensory and non-socketed setae, plumose setae lacking; claw inserted terminally, reflexed, minute and without teeth. Lengths (femur-tarsus) 1.00, 0.77, 0.69, 0.79. Ratios patella-tibia 1.12, patella to tarsus 0.97.

*Legs*. Unarmed, femora and tibiae with short setose spines, metatarsi and tarsi with fine minute setae; tarsal formula: 30,57,28-30,33. Measurements (Paralectotype, FIS Lfd 2937):

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 2.65 | 5.09 | 2.73 | 4.75 |
| Tibia | 2.50 | 4.21 | 2.32 | 3.17 |

*Penis*. Shaft widened basally, glans bent dorsally, rigidly attached to glans; stylus a tightly coiled tube; no bristles or barbed process present near shaft-glans junction.

**Description. Females.** Similar to male except in the following: body larger; pedipalp longer, patella and tibia more robust and with denser pile of setae; legs shorter. Key measurements: BL 3.75, greatest width 2.05, PFL 1.20, LFL 4.15, LTL 2.95.

*Genitalia*. Ovipositor not highly sclerotised; with 18 or 19 segments plus 3 elongate furcal segments, slit sensilla 1-1/1-1 on second furcal segment; few setae on terminal 6-9 segments (including furca). Two seminal receptacles consisting of relatively short loops; weakly sclerotised, only distal triangular region darkly pigmented.

**Comments.** Lawrence (1931) reported secondary sexual characters of the male were absent. Our examination reveals males and juveniles are easily identified from an external examination, as the pedipalps are not as thick as in females.

Kauri (1961: fig.82b) described a juvenile with a double row of teeth on the chelicerae. Among the material at FIS is a juvenile which shows this same pattern - one of the two rows of teeth is on the old cuticle, whereas the second row is visible on the newly forming cuticle. Presumably the specimen Kauri examined had thicker cuticle, because in the juvenile we examined the tips of the shorter cheliceral jaws are also easily observed. Martens' (1978) statement that the teeth are doubled is presumably based on Kauri's description.

**Distribution.** Known only from western Cape Province, Republic of South Africa (Fig.1).

## Ballarrinae n.subfam.

**Diagnosis.** Patella and tibia lacking dense pile of setae, dorsal angle between them less than 180°; tarsus with plumose setae along all or virtually all its length, non-socketed setae restricted to area of distal tip or lacking, femur of leg II with pseudoarticulations in some species.

**Description.** Body small, usually greater than 0.8 and less than 3.5 mm long. Integument usually thin, at the most armed with minute setae. Abdominal spiracle usually concealed beneath coxae IV. Penis shaft usually with strong dorsal keel, muscle usually long (tendon short), left ventrolateral barbed process present or lacking. Ovipositor with 2 or 4 seminal receptacles. Pedipalp patella longer than tibia and usually longer than tarsus, dorsal angle between patella and tibia less than 180°, patella and tibia without dense pile of setae; tarsus usually concave dorsad along its length, plumose setae extend to or almost to distal tip, non-socketed setae restricted to area of distal tip or lacking; tarsal claw lacking, or small, usually inserted ventrodistally, usually with 1 ventral tooth. Chelicerae small in most species; first segment with or without a ventral spur; jaws with continuous row of teeth of subequal size in most species. Legs long and usually slender; pseudoarticulations present in all metatarsi, tibia II, and femur II in some species; tarsi each with a simple claw or a claw with small teeth on each side. Sexual dimorphism slight in most species.

**Subordinate taxa.** *Ballarra* n.gen., *Plesioballarra* n.gen., *Arrallaba* n.gen., *Vibone* Kauri, 1961, *Americovibone* n.gen.

**Comments.** *Ballarra* n.gen., has been chosen as the type genus for the new subfamily as it is the best known taxon in the group with six newly described species; other genera are monotypic. *Vibone* Kauri was described from a single female without the benefit of SEM and this holotype has apparently been lost (L. Cederholm, personal communication). *Americovibone* n.gen., may prove to be representative of a radiation of species in South America. Its characters, including absence of a barbed process on the penis, two spermathecae and the distinctive form of the leg claws may well warrant separate subfamily status when the fauna is better known.

## Key to Ballarrinae n.subfam.

1. First segment of chelicera with ventral process (Fig.23F); leg claws with accessory teeth (Fig.23H,I) ..... *Americovibone*

—— First segment of chelicera without ventral process; leg claws without accessory teeth ..... 2

2. Ovipositor with 2 spermathecae (Kauri, 1961: fig.84e) ..... *Vibone*

—— Ovipositor with 4 spermathecae (Fig.3) ..... 3

3. Tarsus concave dorsad from end to end; plumose setae extending to distal tip (Fig.6E) ..... 4

—— Tarsus not uniformly concave dorsad; plumose setae not extending to distal tip (Fig.21C,D) ..... *Plesioballarra*

4. Dorsum with heavily pigmented mesial stripe (Fig.22B); stylus of penis short and twisted, barbed process longer than glans (Fig.22E,F) ..... *Arrallaba*

—— Mesial stripe, if present, silvery; stylus long and gently curved, barbed process shorter than glans (Fig.8C,D) ..... *Ballarra*

### *Ballarra* n.gen.

**Type species.** *Ballarra drosera* n.sp by original designation.

**Diagnosis.** Dorsum lacks prominent heavily pigmented mesial stripe; pedipalp tarsus concave dorsad and subequal to or shorter than patella, plumes usually restricted to brush at setal tip; stylus usually sub-equal to or longer than glans, barbed process much shorter than glans.

**Description.** Body usually small and soft, unarmed except for scattered small setae; eyemound rounded, unarmed, interocular groove usually shallow or only present posteriorly; dorsum often with mesial silvery patches which may coalesce into an irregular stripe; spiracle with either flattened spines or spines essentially round in cross-section, spines on anterior wall generally more strongly developed, spines virtually lacking in *B. alpina*; chelicerae in both sexes of similar size except for *B. molaris* where greatly enlarged in males; patella subequal to or longer than tarsus, tarsus curved distad, plumose setae extend to tarsal tip, sensory setae few and restricted to extreme tarsal tip, non-socketed setae present distoventrally and/or terminally, not forming a complete subdistal ring, or non-socketed setae absent, claw tiny, reflexed and inserted ventrodistally, or absent; metatarsi and tibia II in all species and femur II in some species with pseudoarticulations; leg tarsi with 15 or more articles; penis with stylus usually subequal to or longer than glans, barbed process much shorter than glans, barbs few or numerous; ovipositorcorpus of more than 2 segments, lateral seminal receptacles penetrate 4-10 segments, dorsal and ventral penetrate 2-3 segments; furca with 3 segments, second with 1-1:1-1 slit sensilla.

**Etymology.** Aboriginal word for spear barbs, alluding to the barbed process on the penis which is characteristic of Australian species in the subfamily. Feminine in gender.

**Distribution.** Eastern mainland Australia from southern Queensland to northern Victoria, and Western Australia.

**Key to *Ballarra* n.gen.**

1. Leg II femur with pseudoarticulations (often difficult to see in faded specimens) ..... 2

—— Leg II femur without pseudoarticulations ..... 5

2. Leg II femur with greater than 5 pseudoarticulations; pedipalp claw lacking ..... *B. clancyi*

—— Leg II femur with less than 5 pseudoarticulations; pedipalp claw minute ..... 3

3. Barbed process on penis bent perpendicular to long axis of penis (usually visible through integument) (Figs 11-12) ..... *B. cantrelli*

—— Barbed process on penis sub-parallel to long axis of penis (usually visible through integument) (Fig.7) ..... 4

4. Sclerotised rim of spiracle usually clearly seen against pale abdomen using stereomicroscope; under SEM anterior rim essentially lacking spines ..... *B. alpina*

—— Sclerotised rim of spiracle usually not easily seen, under SEM anterior rim with a few flattened spines ..... *B. drosera*

5. Pedipalp long (femur sub-equal to body length), coxa without denticulate process near the mouth ..... *B. longipalpus*

—— Pedipalp shorter (femur less than 75% body length), coxa with large denticulate process near the mouth (Fig.16C) ..... *B. molaris*

### *Ballarra drosera* n.sp.

Figs 6E-G, 7-9

**Type material.** HOLOTYPE: AM KS 19434, Budthingeroo Creek, Boyd Plateau, Kanangra-Boyd National Park, via Jenolan Caves, NSW, 33°54'S 150°02'E, near pluviometer, under log, *Eucalyptus fastigata - E. dalrympleana - E. viminalis* forest, G.S. Hunt, 7 Aug. 1987; 1M. PARATYPES: AM KS 19435, same data; 1F. AM KS 19436, same data; 1M. AM KS 19437, same locality, 17 Mar. 1988; 2F. AM KS 19438, same locality, G.S. Hunt, T. Grant & C. Bradley, 11 June 1972; 4M,2F. JCC, same data, 2M,2F. AM KS 19439, same locality, G.S. Hunt, 15 Aug. 1972; 1F. AM KS 19440, same locality, 22 July 1972; 1F. AM KS 19441, same locality, 1 July 1972; 2M. AM KS 19442, Blood Filly Creek, Boyd Plateau, Kanangra-Boyd National Park, NSW, 33°53'S 150°04'E, in grass, *E. fastigata - E. viminalis* forest, M.R. Gray, G.S. Hunt, J. McDougal, 27 Mar. 1976; 1F. AM KS 21666, Jenolan Caves, NSW, 33°49'S 150°02'E, Playing Fields area, *E. viminalis* forest, pit-trap, G.S. Hunt, 15 June - 27 July 1989; 1M. AM KS 19443, Lithgow, NSW, hillside in valley in north-east corner of town, under log, *Eucalyptus* forest, 33°29'S 150°10'E, G.S. Hunt, 2 July 1972; 1F.

**Other material examined.** AM KS 19431, Bondi State Forest, south-south-east of Bombala, NSW, 37°08'S 149°09'E, "woodlot 1" of 1980 Australian Museum ecological study, under logs in shallow grassy valley, G.S. Hunt, 6 Apr. 1988; 1M,1F. AM KS 19432, same data; 3M,3F. AM KS 11345, same locality, woodlot 1, Australian Museum ecological study, litter berlesate, 27 Sept. 1980; 1M,2F. AM KS 11984, same data, 4 July 1980; 1F. AM KS 19447, Mount Wog Wog, 17km south-east of Bombala, NSW, 37°04'S 149°28'E, CSIRO survey, C.R. Margules, July 1987; 6M,4F. AM KS 19448, same data, Oct. 1987; 1F,1J.

**Diagnosis.** Bars of pigment on abdomen penetrated by mesial silvery patch; spiracle occluded by a few flattened spines rather than numerous elongate spines rounded in cross-section; pedipalp tarsus with non-socketed setae distoventrally and terminally, claw with

ventral tooth; barbed process not strongly bent across axis of penis shaft, barbs greater than 10 and less than 20.

**Description. Males** (Boyd Plateau population). *Body*. BL 1.14, CTW 0.83-0.96 (mean 0.90, n = 8). Dorsal pattern (recently collected specimen) as figured, mesial bars of dark brown pigmentation reflecting segmentation, each penetrated by a mesial silvery patch fully enclosed by the pigment; dorsum with irregular silvery stripe placed more laterally. Venter very light brown, abdomen darker laterally and posteriorly; intersternite sutures silvery. Anterior margin not deeply indented. Eyemound mostly black, low, up to 0.7 its length from anterior margin, slightly steeper anteriorly than posteriorly, unarmed; interocular groove shallow. Coxobuccal region as figured; endites, labrum and labium not heavily sclerotised.

*Spiracle*. Length 0.030, width 0.012. Spines on anterior wall broad and flat, some with multiple terminations; posterior wall relatively unarmed. Rows of micro-ornamentation anterior to spiracle poorly developed; posterior micro-ornamentation well developed but irregular, replaced more posteriorly by rows of linguoform-globular papillae.

*Chelicerae*. Brown, gracile. Teeth as in Figure 8G, subequal. CSL 0.57-0.67 (0.62).

*Pedipalps*. Very dark brown, slender. Plumose setae as figured. Non-socketed setae on tarsus placed distoventrally; tarsal claw tiny, with ventral tooth. PFL 0.89-1.00 (0.95), ratio patella-tibia 2.22-2.44 (2.27), patella to tarsus 1.19-1.32 (1.23). Femur-tarsus lengths (of holotype): 1.04, 0.69, 0.26, 0.58.

*Legs*. Femora brown but darker subdistally, femur IV with dark sub-proximal band; patellae, metatarsi and tarsi almost black; metatarsi with prominent distal silvery band. Femur II with 2-3 pseudoarticulations. Tarsi not minutely divided into articles, only 3 articles very short. Tarsal formula: 16, 27-31, 13-18, 16-18. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 1.40 | 3.55 | 1.23 | 2.64 |
| Tibia | 1.13 | 3.50 | 1.02 | 1.64 |

*Genitalia*. PL 0.96; ratio shaft:glans:stylus 0.51:0.22: 0.26. Barbed process slender, axis sub-equal to shaft axis; barbs moderately numerous (15-16, n = 2), terminal barb elongate. Basilateral flanges of stylus as figured, basiventral flanges almost absent.

**Description. Females.** Similar to male except in the following: body larger, CTW 0.89-1.15 (1.07, n = 7);

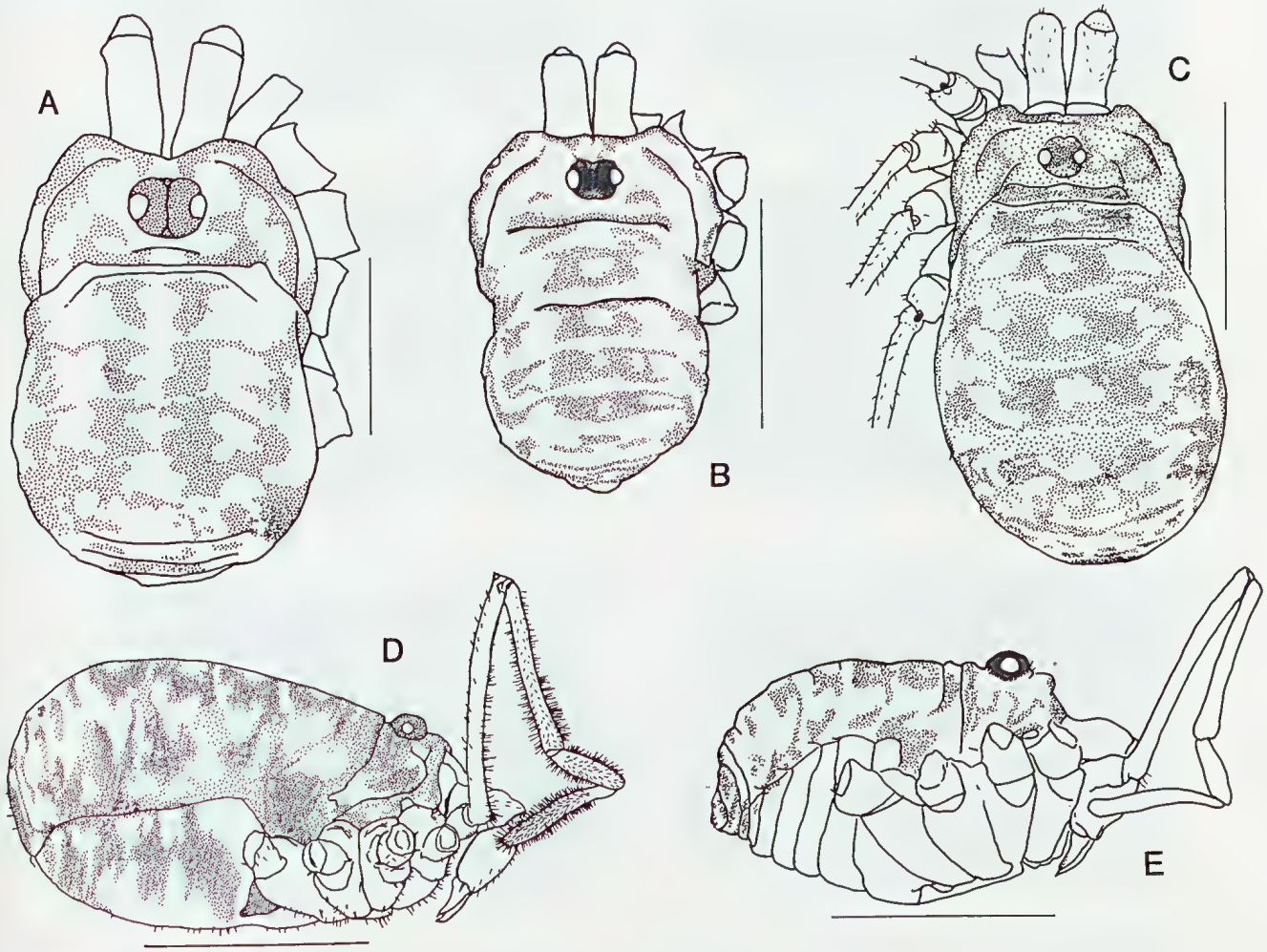


**Fig.7.** *Ballarra drosera* n.sp. A. Body of paratype male *ex* Bondi State Forest, dorsal; B,E. Male *ex* Boyd Plateau, dorsal & lateral; C,D. Female *ex* Boyd Plateau, dorsal & lateral. Scale bars 0.5 mm.

chelicera and pedipalp relatively longer, legs relatively shorter. Tarsal formula: 15-17,24-33,15-16,15-19. Key measurements: BL 1.42, CTW 0.90, CSL 0.72, PFL 1.19, LFL 3.15, LTL 3.02.

*Genitalia.* Ovipositor as figured; lateral spermathecae penetrate 7 segments; dorsal and ventral spermathecae penetrating 3 segments.

**Variation.** The Bondi State Forest population differs from the Boyd Plateau population in the following: bars of pigment on abdomen more disrupted laterally and mesially by silvery-gold areas, mesial

**Fig.8.** *Ballarra drosera* n.sp. A. Ovipositor; B. Detail of seminal receptacles; C,D. Penis, ventral & lateral. E,G. Female chelicera, retrolateral & dorsal, F. Male chelicera, retrolateral; H. Coxal and buccal region, female. I. End of tarsus of leg 1, retrolateral. Scale bars 0.1 mm.

silvery-gold patches tend to coalesce to form a stripe; integument anterior to spiracle with narrow zone of micro-ornamentation, posterior to spiracle micro-ornamentation sharper and more clearly defined; penis with barbed process slightly more robust and with terminal barb shorter, basiventral flanges of stylus moderately well developed. The Mount Wog Wog population resembles that of Bondi State Forest except

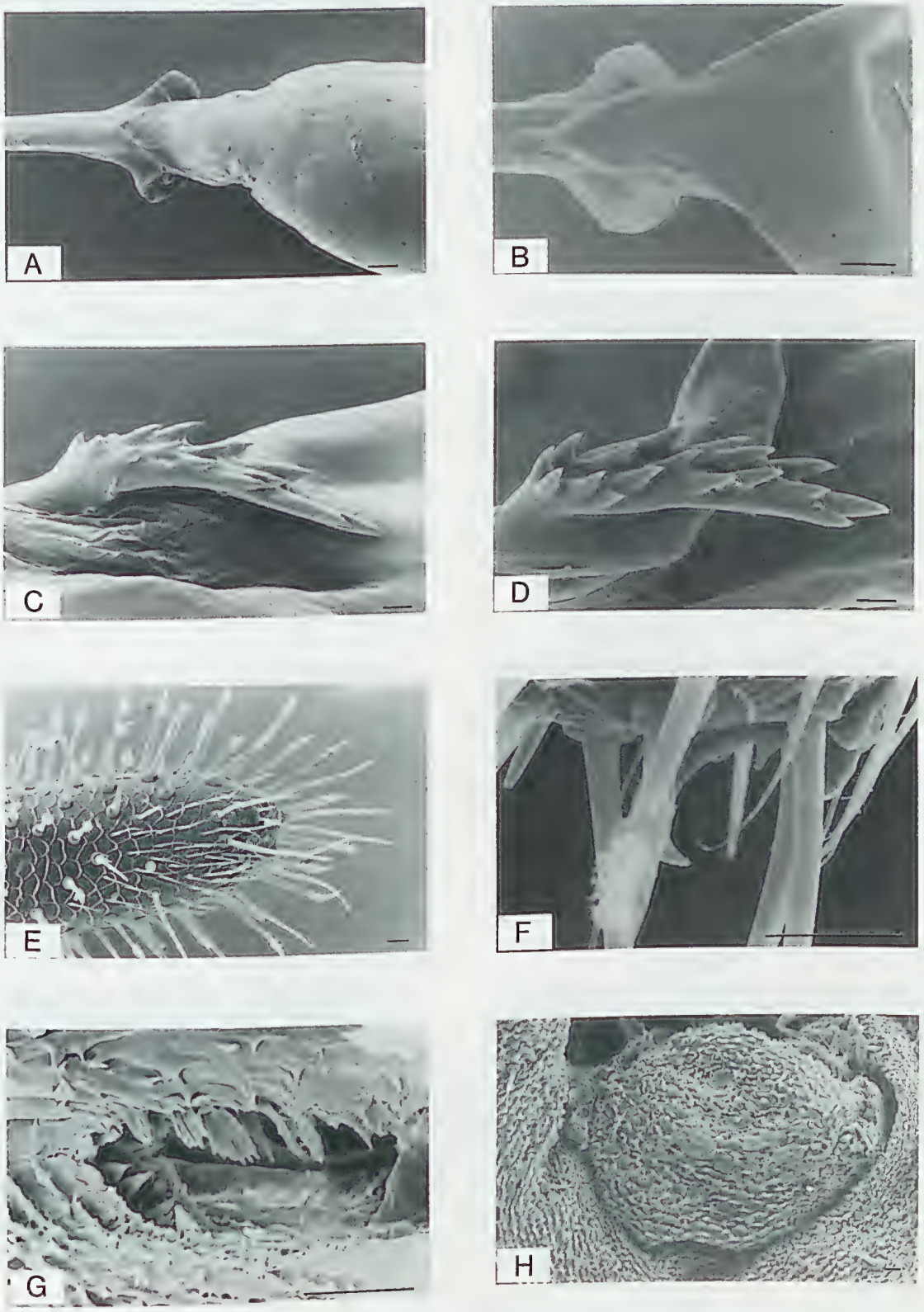


**Fig.9.** *Ballarra drosera* n.sp. A-D. Detail of penis, ventral: A,C. Base of stylus & barbed process *ex* Boyd Plateau; B,D. *ex* Bondi State Forest; E. Tip of pedipalp tarsus, retroventral; F. Detail of pedipalp claw, lateral; G. Detail of spiracle spines. H. Anal operculum and vestige of corona analis, male. Scale bars 10 µm.

that many individuals have attenuated pedipalps.

**Comments.** *Ballarra drosera* is most closely related to *B. alpina* n.sp.; somewhat less so to *B. cantrelli*, n.sp., and *B. clancyi*, n.sp. Differences shown by the southern populations (Bondi State Forest and Mount Wog Wog) may warrant separate species status but a decision should await further study including that of intervening populations.

Since going to press, specimens of a new species from the Adelaide region, South Australia, have been found in the South Australian Museum's collection. This species is close to *B. drosera.*

**Etymology.** The specific epithet refers to the dew-like secretory droplets on the pedipalp setae, in life reminiscent of sticky hairs on the carnivorous plant *Drosera.*

**Natural history.** Adults have been collected from March-August (Boyd Plateau) and April-October (southern populations). Under logs; tends to occur near the boundary between the saturated and dry parts of the log (Hunt, 1979).

**Distribution.** New South Wales: western Blue Mountains from Boyd Plateau to Lithgow, and Monaro region in the south-east of the State.

### *Ballarra alpina* n.sp.

Figs 10, 11A-D

**Type material.** HOLOTYPE: AM KS 19136, Smiggin Holes, Kosciusko National Park, NSW, 36°24'S 148°26'E, snow gum (*Eucalyptus pauciflora*) woodland near quarry, 1700 m, under logs & in litter, G.S. Hunt & M.M. Zabka, 5 Apr. 1988; 1M. PARATYPES: AM KS19137, same data; 1F. AM KS19138, same data; 2M, 1F.

**Additional material examined.** AM KS19139, Mount Kosciusko area, Kosciusko National Park, NSW, open snow gum woodland, 1800 m, K. Green, 1987; 4M,1F,3J (specimens damaged).

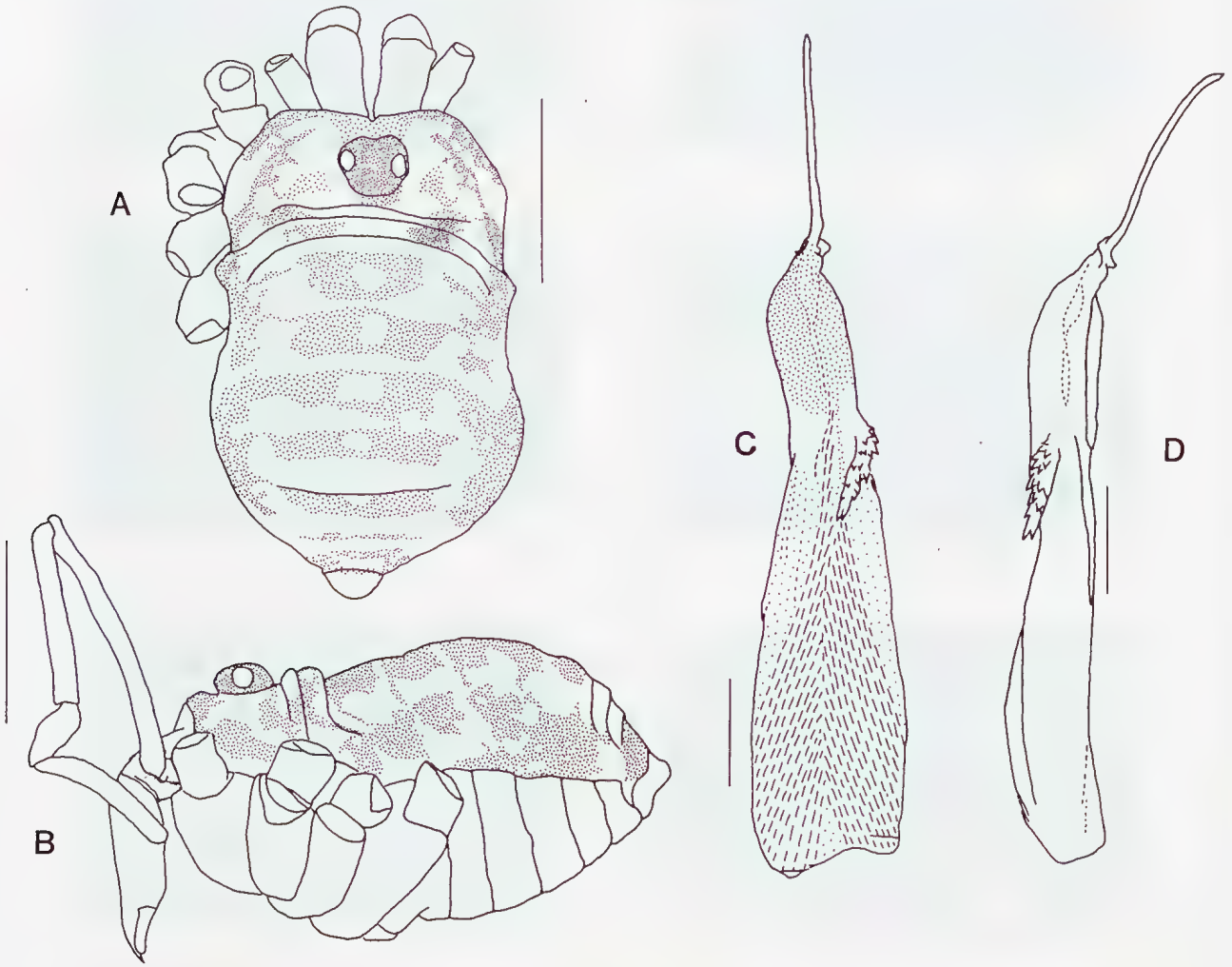


**Fig.10.** *Ballarra alpina* n.sp. A,B. Body, dorsal & lateral of male; C,D. Penis, ventral & lateral. Scale bars: A,B = 0.5 mm; C,D = 0.1 mm.

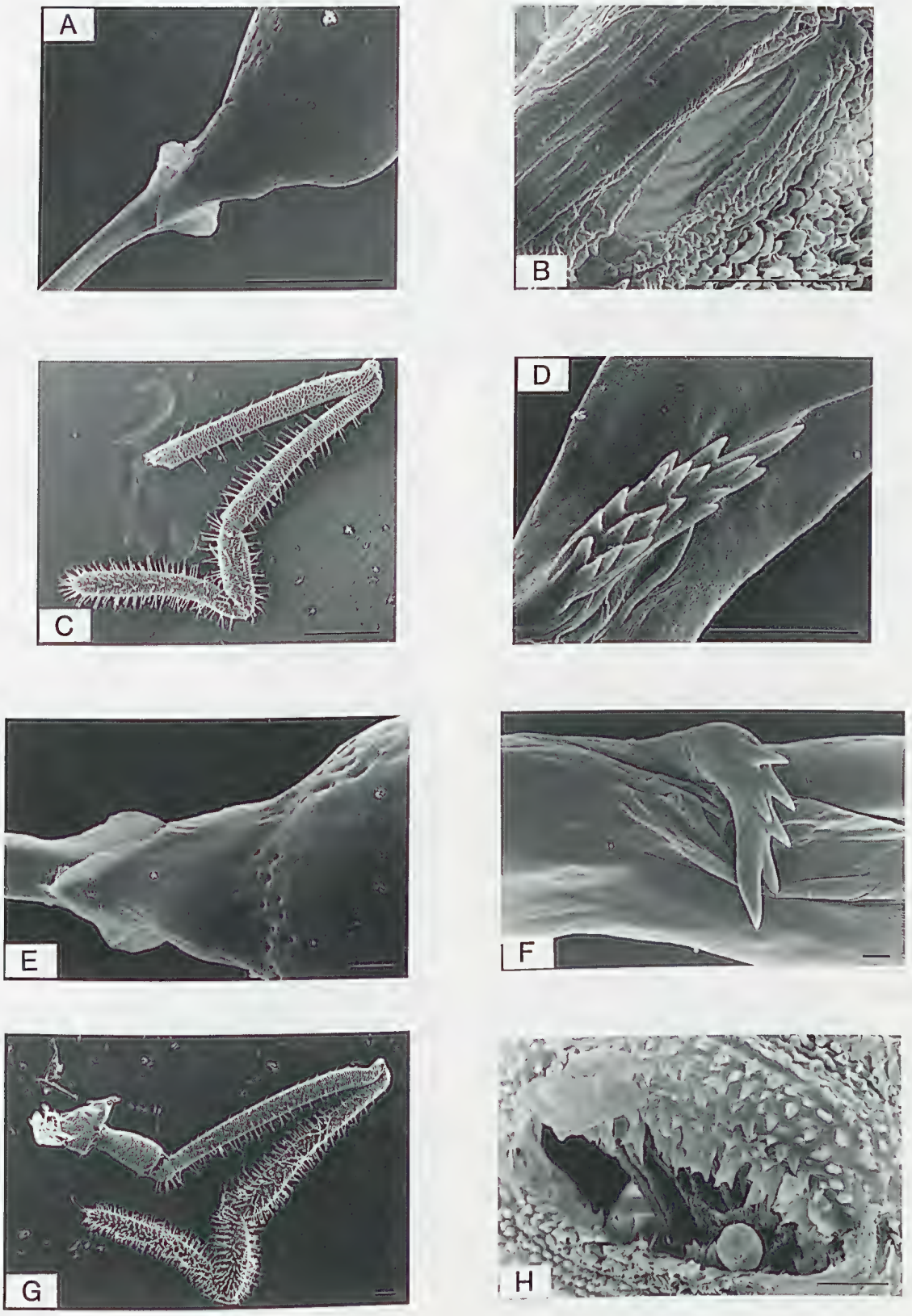


**Fig.11**. *Ballarra* spp. A-D. *B. alpina* n.sp.; E-H. *B. cantrelli* n.sp. A,E. Base of stylus, ventral; D,F. Barbed process, ventral; C,G. Pedipalp, retrolateral; D,H. Spiracle. Scale bars: A,B = 50 μm; C = 200 μm; D = 20 μm; F,H = 10 μm; G = 100 μm.

**Diagnosis.** Similar to *B. drosera* but spiracle easily seen against paler abdomen and almost without occluding spines, and barbs on penis barbed process more numerous.

**Description. Males.** *Body.* BL 1.43, CTW 0.83. Dorsal pattern as figured, similar to *B. drosera* except that mesial silvery patches slightly smaller and some not completely enclosed anteriorly by pigment. Otherwise similar to *B. drosera* except that eyemound closer to anterior margin, eye set high on eyemound, interocular groove moderately deep.

*Spiracle.* Length 0.041, width 0.009. Clearly visible against pale abdomen. Spines on anterior and posterior wall almost completely lacking; integument anterior to spiracle essentially smooth, micro-ornamentation poorly developed immediately posterior to spiracle but followed by very broad linguoform grading posteriorly to narrow linguoform papillae.

*Chelicerae.* Form similar to *B. drosera.* CSL 0.62.

*Pedipalps.* Form and setal disposition similar to *B. drosera.* Lengths (femur-tarsus) 0.83, 0.55, 0.25, 0.47. Ratios patella to tibia 2.20, patella to tarsus 1.17.

*Legs.* Form similar to *B. drosera*; femora through metatarsi with prominent distal silvery patch; tarsal formula: 15, 25-26,15,17. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 1.24 | 2.94 | 1.29 | 2.18 |
| Tibia | 0.98 | 2.98 | 0.94 | 1.43 |

*Genitalia.* PL 0.58; ratio shaft:glans:stylus 0.53:0.20:0.27. Barbed process about 20° to shaft axis, terminal barb shorter and barbs more numerous (22) than *B. drosera*; basiventral flange of stylus more strongly developed.

**Description. Females.** Sexual dimorphism slight, similar to *B. drosera.* Tarsal formula: 14,26,13,16. Key measurements: BL 2.27, CTW 1.09, CSL 0.70, PFL 0.95, LFL 2.36, LTL 2.46.

*Genitalia.* Lateral receptacles penetrate 8 ovipositor segments; dorsal and ventral 3.

**Comments.** *Ballarra alpina* is very close to the Bondi State Forest population of *B. drosera* but differs markedly in spination of spiracle. The limited collecting data suggest there may be genetic isolation from *B. drosera* due to asynchronous life histories, adults of *B. alpina* being active in warmer months, *B. drosera* in cooler months.

**Etymology.** The specific epithet refers to the high altitude of the type locality in the "Australian Alps".

**Natural history.** Dr Ken Green's ecological study in Kosciusko National Park (Green, 1988) involved pitfall trapping in all seasons 1983 to 1986. Several immatures and some adults were sorted from a single February sample at Smiggin Holes. It is not known if adults hibernate, or whether the species overwinters in the egg or juvenile stage.

**Distribution.** Subalpine areas in Kosciusko National Park, New SouthWales.

### *Ballarra cantrelli* n.sp.

Figs 11E-G, 12

**Type material.** HOLOTYPE: QM S15523, Bald Mountain area, via Emu Vale, Qld, 28°14'S 125°25'E, 1000-1300 m, B.K. Cantrell, 17-22 May 1969; 1M. PARATYPES: QM S15524, same data; 1F. UQ, same data, 1F. UQ, same data; 10M,9F. AM KS 21420, same locality, B.K. Cantrell, 27-31 Jan. 1972; 1M. AM KS 19433, same locality, T. Weir, Feb. 1970; 1F. AM KS5678, Lorne State Forest, via Lorne, NSW, 31°34'S 152°36'E, site 86(5), pitfall trap, D. Milledge, 1 Sept. - 19 Dec. 1979; 1M. AM KS 16064, same site, 29 Oct. - 10 Dec. 1978; 1M,1F. AM KS 15995, same location, site 86(4), 29 Oct. - 10 Dec. 1978; 1F. AM KS 1813, same location, site 87(2), 27 Aug. - 24 Sept. 1978; 1M.

**Diagnosis.** Abdomen without clearly defined mesial silvery patches penetrating bars of pigment; eyes set high and posteriorly on eyemound; pedipalp claw without ventral tooth; barbed process bent perpendicular to penis shaft, 4-6 barbs; stylus extremely long.

**Description. Males.** *Body.* BL 1.52, CTW 0.78. Dorsal pattern as figured; abdomen with heavy dark brown pigmentation mediodorsally interrupted by thin transverse silvery stripes/patches and flanked laterally by longitudinal silvery zone; cephalothorax predominantly pale. Sternites strongly pigmented except at sutures. Anterior margin not strongly indented. Eyemound black, low, unarmed; eyes large, set high and posteriorly on eyemound; interocular groove shallow. Endites, labium and labrum not heavily sclerotised.

*Spiracle.* Length 0.050, width 0.020. Spines on anterior wall broad and flattened, usually terminally bi- or multifurcate; posterior wall with smaller and fewer spines. Narrow zone of strong micro-ornamentation anterior to spiracle; posteriorly rows of lamellate micro-ornamentation succeeded by closely spaced papillae not as globular as in *B. drosera.*

*Chelicerae.* Gracile; teeth delicate and nearly equal in size. CSL 0.64.

*Pedipalps.* Tarsus with non-socketed setae distoventrally and at tip; claw tiny, without ventral tooth. Lengths (femur-tarsus) 0.82, 0.64, 0.27, 0.51; ratios patella to tibia 2.37, patella to tarsus 1.25.

*Legs.* Slender. Femur II with 3 pseudoarticulations, only 3-5 very short articles distally on tarsi. Tarsal formula: 15,31,15,17. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 1.37 | 3.24 | 1.24 | 2.23 |
| Tibia | 1.01 | 3.00 | 1.00 | 1.60 |

*Genitalia.* PL 0.65; stylus very long, ratio shaft:glans:stylus 0.46:0.22:0.32. Barbed process perpendicular to shaft axis; only 4-6 barbs. Basal flanges as figured; basiventral flange well developed.

**Description. Females.** Similar to male except in the following: body larger, appendages relatively shorter. Tarsal formula: 15,26,13,16. Key measurements: BL 1.68, CTW 1.03, CSL 0.60, PFL 0.76, LFL 2.48, LTL 2.27.

*Genitalia.* Ovipositor as figured; lateral receptacles penetrate 8-9 segments; ventral and dorsal 3 segments.

**Comments.** This species is closely allied to *B. drosera*

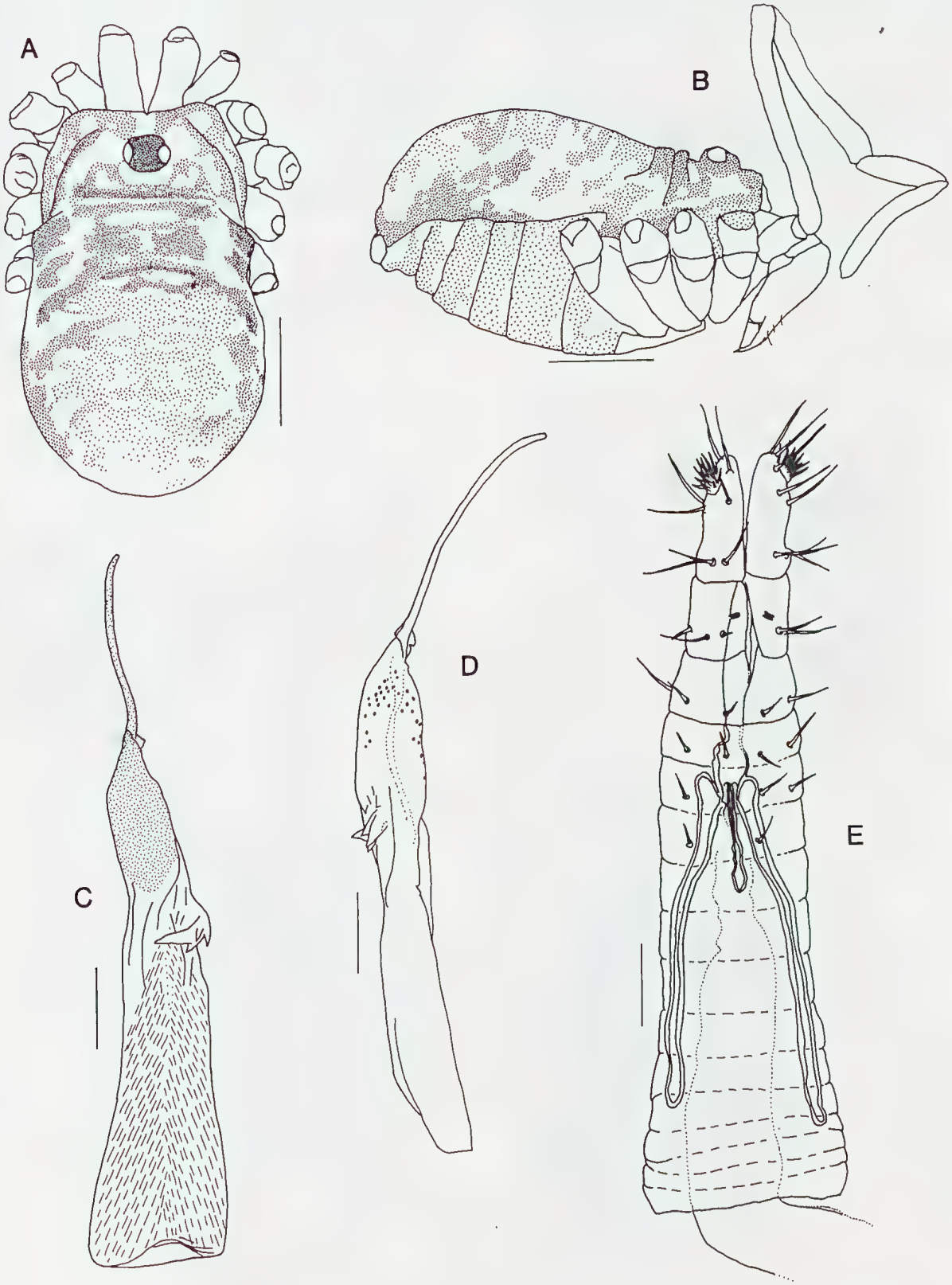


**Fig.12.** *Ballarra cantrelli* n.sp. A,B. Body of female, dorsal & lateral; C,D. Penis, ventral & lateral, E. Ovipositor, ventral. Scale bars: A,B = 0.5 mm; C-E = 0.1 mm.

despite the striking apomorphy of the penis barbed process.

**Etymology.** The specific epithet acknowledges the contribution of Dr Bryan Cantrell to Opiliones research and for collecting most of the specimens of this new species.

**Distribution.** Coastal ranges of eastern Australia from Taree area of New South Wales to Emu Vale area of southern Queensland though apparently not occurring on the Lamington Plateau.

### *Ballarra clancyi* n.sp.

Figs 13, 14, 15A-E

**Type material.** HOLOTYPE: AM KS19122, Lane Cove, Sydney, bushland north side of Epping Road next to Stringy Bark Creek, NSW, 34°47'S 151°08'E, under log, G.S. Hunt, 16 July 1988; 1M. PARATYPES: AM KS 19123, same data, 19 Sept. 1987; 1F. AM KS19124, same data; 1M. AM KS19125; same locality, berlesate NSW Dept of Agriculture Argentine Ant Survey, M.J. Fletcher & G.P. Fitt, 17 June 1987; 1M,3J. AM KS19128, same data, 23 June 1983; 1F,3J. AM KS 19126, Wyong, NSW, 33°17'S 151°26'E, crack in garden path, J. Clancy, 13 Aug. 1987; 1F. AM KS 19127, same locality, in kitchen, J. Clancy, 18 Aug. 1987; 1F.

**Additional immature material examined.** AM KS 19129-35, numerous immatures, type locality.

**Diagnosis.** Abdomen dorsum extensively pigmented but with many small silvery patches; eyemound set less than 0.5 its length from strongly indented anterior margin; pedipalp tarsus curved strongly dorsad, lacking

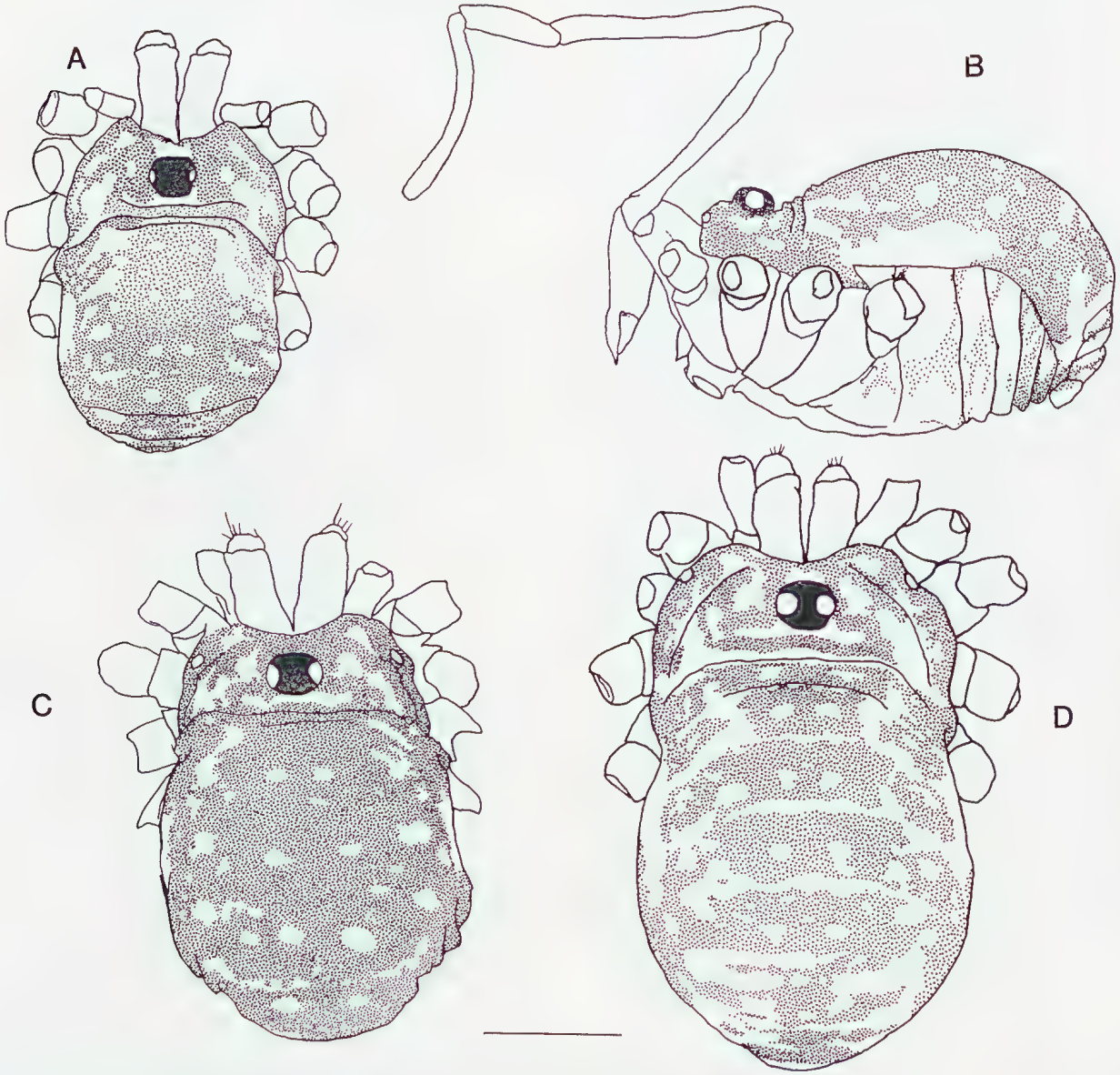


**Fig.13.** *Ballarra clancyi* n.sp. A,D. Male & female *ex* Lane Cove, dorsal; B,C. Female *ex* Wyong, lateral & dorsal. Scale bar 0.5 mm.

non-socketed setae and claw; barbed process of penis broad distally, greater than 30 barbs; femur of leg II with 7-9 conspicuous pseudoarticulations.

**Description. Males.** *Body.* BL 1.45, CTW 0.86. Dorsal colour pattern (freshly killed specimen) as figured; abdomen largely dark purplish-brown penetrated by silvery spots and patches, bars of pigment across each segment tending to have a pair of mesial silvery spots. Venter paler. Anterior margin strongly indented above chelicerae. Eyemound black, relatively large, unarmed, set only about 0.4 its length behind anterior margin; eyes large; interocular groove shallow. Endites, labium and labrum not heavily sclerotised.

*Spiracle.* Length 0.062, width 0.015. Spines on anterior wall more numerous and rounded in cross-section than *B. drosera*, usually with 1 or 2 terminations; spines on posterior wall numerous but very short. Integument anterior to spiracle folded but virtually without micro-ornamentation; posterior to spiracle with rows of sharp micro-ornamentation; more posteriorly micro-ornamentation tends to be bluntly conical and less globular than in *B. drosera.*

*Chelicerae.* Gracile; denticles on dorsal surface strong; teeth subequal; CSL 0.80.

*Pedipalps.* Very dark brown. Long and slender. Tarsus very strongly curved dorsad; non-socketed setae and claw lacking. Many of the setal plumes appear to be trifid. Lengths (femur-tarsus) 1.05, 0.82, 0.39, 0.69. Ratios patella to tibia 2.10, patella to tarsus 1.19.

*Legs.* Dark brown. Femur II with 7-9 pseudoarticulations. Tarsus II distally with numerous

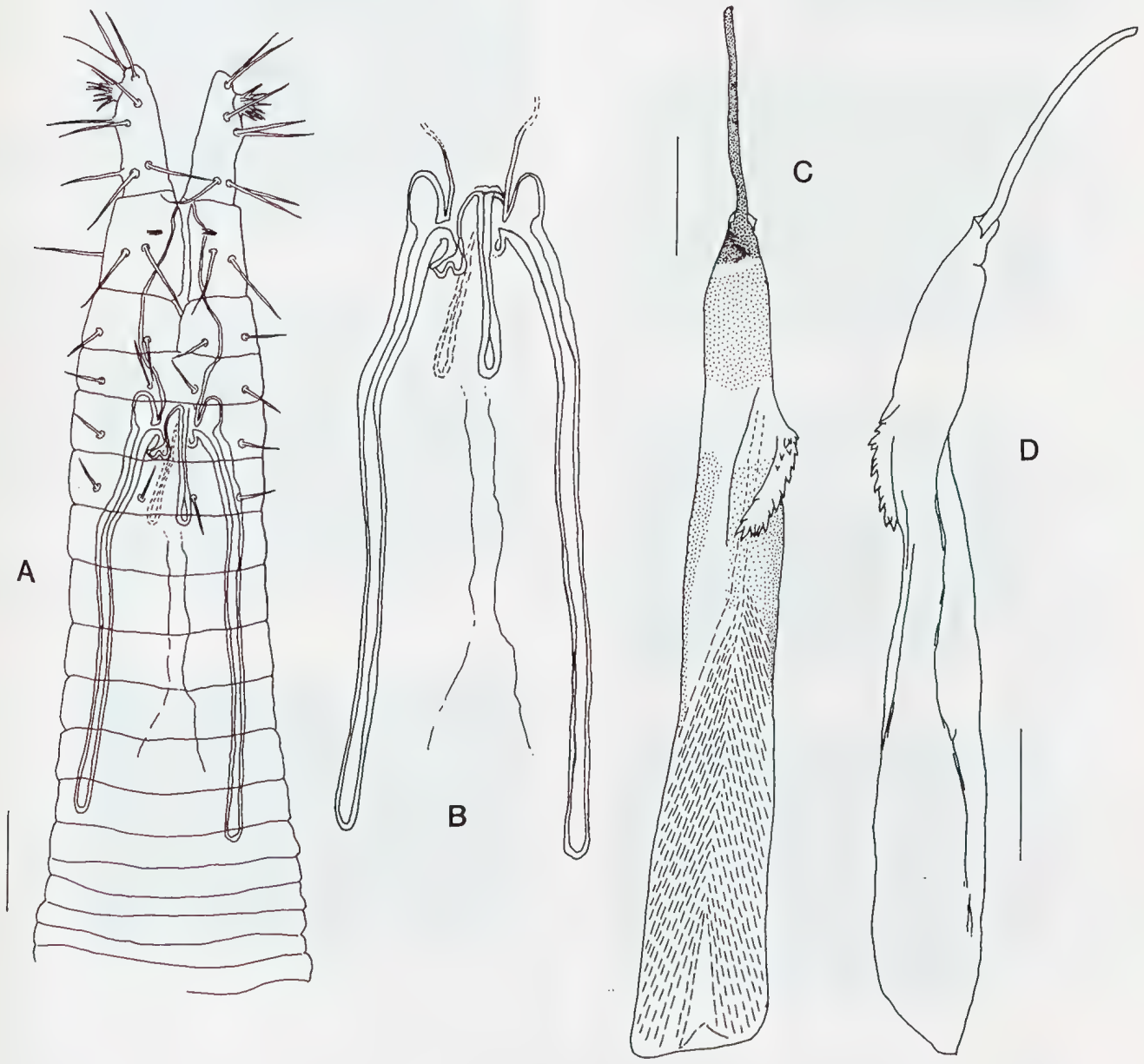


**Fig.14.** *Ballarra clancyi* n.sp. A. Ovipositor, ventral; B. Detail of seminal receptacles; C,D. Penis, ventral & lateral. Scale bars 0.1 mm.

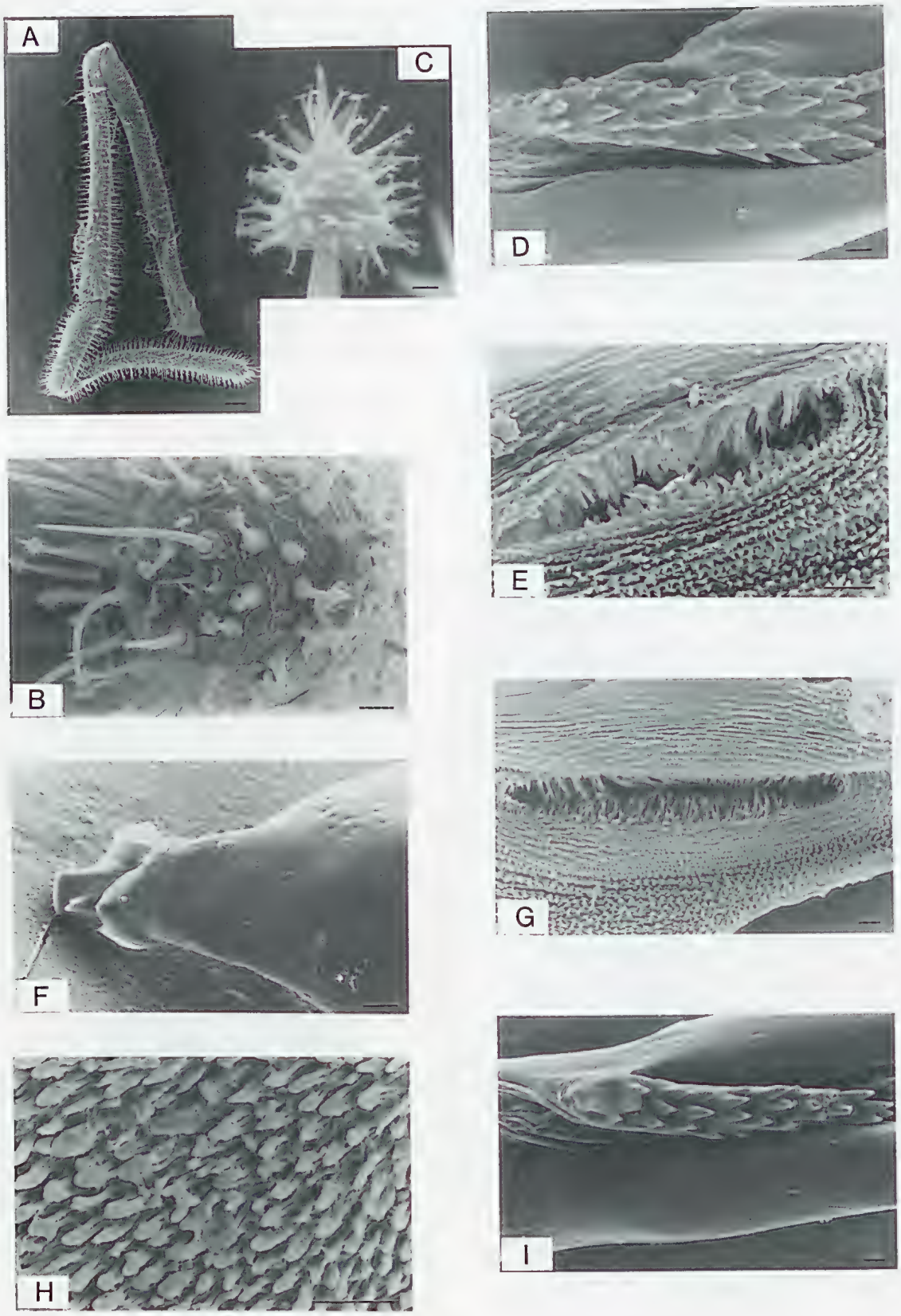


**Fig.15.** *Ballarra* spp. A-E. *B. clancyi* n.sp.; F-I. *B. molaris* n.sp. A. Pedipalp, retrolateral; B. Tip of tarsus, end view; C. Detail of plume brush on plumose seta; D,I Barbed process of penis, ventral; E,G. Spiracle. F. Base of stylus (stylus broken), ventral; H. Microsculpture of integument posterior to spiracle. Scale bars: A = 100 µm; C = 1 µm; others 10 µm.

short articles; other tarsi distally with 3 short articles. Tarsal formula: 20,50,17,19. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 2.13 | 4.82 | 2.04 | – |
| Tibia | 1.64 | 4.66 | 1.58 | – |

*Genitalia.* PL 0.85; ratio shaft:glans:stylus 0.61:0.17:0.22. Barbed process wide distally, axis at about 25° to shaft axis; barbs very numerous (35).

**Description. Females.** Similar to male except in the following: dorsal pigmentation of Paratypes KS 19123 and KS 19126 with abdomen more broken by transverse silvery stripes though KS 19127 similar to male. Body larger, pedipalp and legs shorter. Tarsal formula: 17,44,17,18. Key measurements: BL 2.42, CTW 1.10, CSL 0.84, PFL 1.37, LFL 3.88, LTL 3.69.

*Genitalia.* Ovipositor as figured; lateral receptacles penetrate 9-10 segments; ventral and dorsal 3 segments.

**Variation.** Colour pattern varies between Wyong and Lane Cove individuals (Fig.13) but larger samples are needed to determine whether this is intra- or interpopulational variation.

**Comments.** This species, like *B. molaris*, has the most apomorphic pedipalp in the genus in terms of the combination of curvature of the tarsus, loss of claw and non-socketed setae and restriction of plumes to a brush at the setal tip.

**Etymology.** The specific epithet acknowledges the collecting work of Mr John Clancy which drew our attention to the existence of this species in the Sydney region.

**Natural history.** Numerous juveniles were present in berlesates taken in autumn-early winter 1983. Adults have been collected in winter-spring.

**Distribution.** Sydney region, New South Wales.

### *Ballarra molaris* n.sp.

Figs 15F-I, 16, 17

**Type material.** HOLOTYPE: MOV K0904, Liparoo State Forest, west of Wemen, 7.9 km north-west of junction of Mid-Victorian Highway & Annuello Road, Vic, 34°46'S 142°33'E, LCC Mallee Survey, site 17, young-medium River Red Gum (*Eucalyptus camaldulensis*) near Murray River, a few large trees, grass understorey, drift fence pitfall trap, A.L. Yen, Sept. 1986; 1M. PARATYPES: MOV K0906, same data; 1F. AM KS 19140, same data; 1M,1F. MOV K0907-14, same data; 7M,1F. MOV K0905, Liparoo State Forest, 9.7 km north-west of junction of Mid-Victorian Highway & Annuello Road, Vic, 34°45'S 142°32'E, LCC Mallee Survey, site 20, on bank of Murray River, River Red Gum with sparse grass and herb understorey, altitude 60 m, drift fence pitfall trap, A.L. Yen, Sept. 1986; 1M. PARATYPE: ANIC, Beelbangera, NSW, 34°15'S 146°06'E, F.J. Gay, 8 July 1969; 1M.

**Diagnosis.** Relatively large; male chelicerae large with greatly enlarged tooth on each finger; pedipalp coxa with incrassate denticulate process prolaterally, pedipalp tarsus without claw; leg tarsi finely subdivided into numerous short articles; spines on posterior wall of spiracle better developed than anterior; stylus and glans subequal in length, stylus with sharp tooth distal to basoventral flange.

**Description. Males.** *Body.* BL 2.62, CTW 1.95. Dorsal pattern (recently collected specimen) as figured; abdomen with mesial bars of pigment broken by silvery patches and flanked by semicontinuous silvery zone with heavily pigmented patches more laterally; eyemound surrounded by pale zone. Sternites predominantly silvery in some individuals, heavily pigmented in others. Some individuals very melanic. Cephalothorax high and much more rigid than abdomen; anterior margin not strongly indented. Eyemound low and placed about its length behind anterior margin; interocular groove absent except posteriorly. Coxobuccal region of Beelbangera specimen as figured: endites of pedipalp and coxa I, labium and labrum heavily sclerotised; pedipalp coxa prolaterally with incrassate, heavily denticulate process; these features less well developed in some Victorian specimens.

*Spiracle.* Very long, length 0.160, width 0.020. Spines on anterior wall not as strongly developed as those on posterior wall; spines long, multiply terminated, not markedly flattened. Spiracle flanked anteriorly and posteriorly by multiple closely spaced rows of sharp micro-ornamentation, replaced well posterior to spiracle by very densely packed linguoform-globular papillae.

*Chelicerae.* Massive, though allometrically smaller in smaller males. Second segment dark brown with black areas; each finger with 1 very large tooth and many small teeth. CSL 2.08.

*Pedipalps.* Tarsus markedly curved dorsad; claw and non-socketed setae apparently lacking. Lengths (femur-tarsus) 1.70, 1.44, 0.58, 0.94; ratios patella to tibia 2.48, patella to tarsus 1.53.

*Legs.* Femora stout except for leg II. Femora dark brown; patellae and tibiae lighter but often dark laterally; metatarsi light; tarsi dark brown-black. Femora lack pseudoarticulations. Tarsi very finely divided with numerous short articles. Tarsal formula: 19,47,17,19. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 1.51 | 3.30 | 1.58 | 2.29 |
| Tibia | 1.27 | 3.41 | 1.25 | 1.74 |

*Genitalia.* PL 1.02; ratio shaft:glans:stylus 0.64:0.17:0.18.

Basilateral flanges asymmetrical, right flange pointed; basiventral flange well developed with small sharp peg distal to it. Barbed process with numerous barbs (29); proximal barbs covered by flap of integument (possibly an artifact).

**Description. Females.** Similar to male except in the following: body longer; chelicerae small with teeth more even in size. Tarsal formula: 15,42,17,17. Key measurements: BL 3.27, CTW 1.51, CSL 1.09, PFL 1.54, LFL 4.12, LTL 4.09.

*Genitalia.* Ovipositor as figured; lateral spermathecae penetrate 8-9 segments; ventral and dorsal penetrate 3.

**Comments.** This species is placed in *Ballarra* on the basis of synapomorphies of the pedipalp, setal plumes and the long stylus and lateral seminal receptacles. A new genus may need to be erected should this highly distinctive species be representative of a radiation of species, for example, along the river systems of inland Australia.

**Etymology.** The specific epithet refers to the denticulate process on each pedipalp coxa which may be used like millstones or nutcrackers to break hard-bodied prey.

**Natural history.** This species, which occurs in semiarid Australia (between 250 and 500 mm rainfall), has been collected between July and August. It is not known whether adults aestivate or whether another life history strategy is employed.

**Distribution.** River Red Gum forest, Murray and

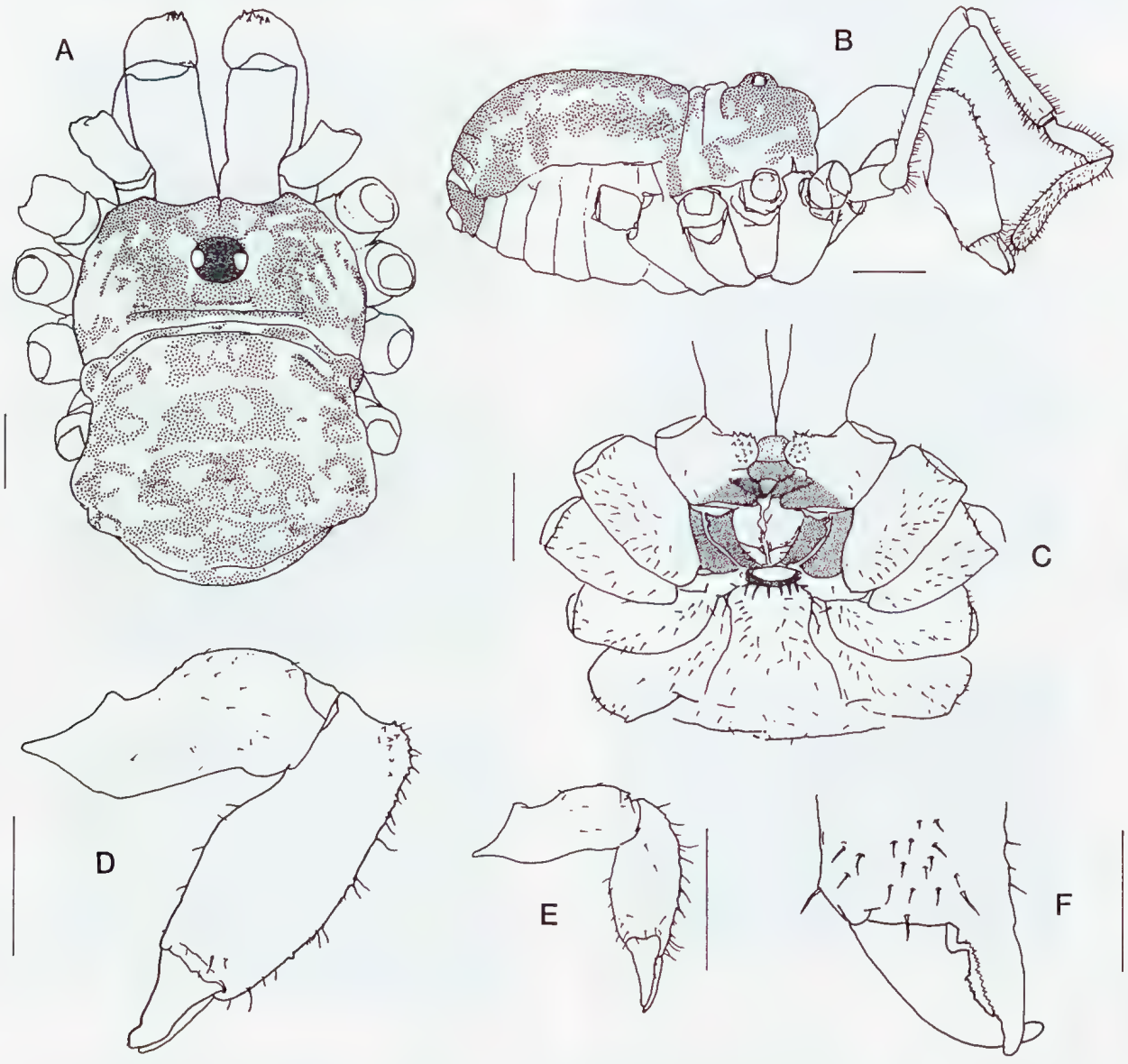


**Fig.16.** *Ballarra molaris* n.sp. A,B. Body, dorsal and lateral; C. Coxal and buccal region, ventral; D,F. Male chelicera, lateral & dorsal view of chelae; E. Female chelicera, lateral. B, *ex* Beelbangera; others *ex* Liparoo State Forest. Scale bars: A-C = 0.5 mm; D-F = 0.1 mm.

Murrumbidgee Rivers, semiarid zone, Victoria and New South Wales.

### *Ballarra longipalpus* n.sp.

Figs 18, 19A-D

**Type material.** HOLOTYPE: WAM 87/1270, 6 km at 15° from Mullaloo Beach, WA, 31°47'S 115°44'E, A. Chapman & R. How, 3-17 Sept. 1978; 1M. PARATYPES: WAM 88/748-9 Reabold Hill, Perth, WA, 31°57'S 115°46'E, pitfall traps (RH6), J.D. Majer, 28 Aug. 1976; 2M. WAM 88/750, same data; 1F. WAM 88/751, same data; 1F.

**Additional material examined.** WAM 88/738-47, Reabold Hill, WA, pitfall traps (RH5), J.D. Majer, 30 June 1976; WAM, 90/1352-3, Perth, Kings Park, WA, ex tree traps, S.J. Curry, 31 July 1978; WAM 88/737, Dwellingup, WA, 32°43'S 116°04'E, Plavins Plots, pitfall traps, S.J. Curry, 28 June 1979; J. WAM 88/132, same locality, S.J. Curry, 29 July 1977; J. WAM 55/5001-2, Gosnells, WA, 32°05'S 116°00'E; 1M,1F (damaged). WAM 87/1271, 1301, Porongorups, WA, 34°42'S 117°53'E, *Eucalyptus diversicolor* Karri-*Acacia* understorey, J.A. Springett, 13 Apr. 1971; WAM, 90/1222, 5 km north-east of Mount Lesueur, 30°10'S 115°15'E, pit-trap, J. Gaull & Party, 13 July 1990, F.

**Diagnosis.** Pedipalp extremely long and thin; pedipalp tarsus curved distad, non-socketed setae very few and at extreme tip of tarsus, claw lacking; seminal receptacles penetrate 4 ovipositor segments.

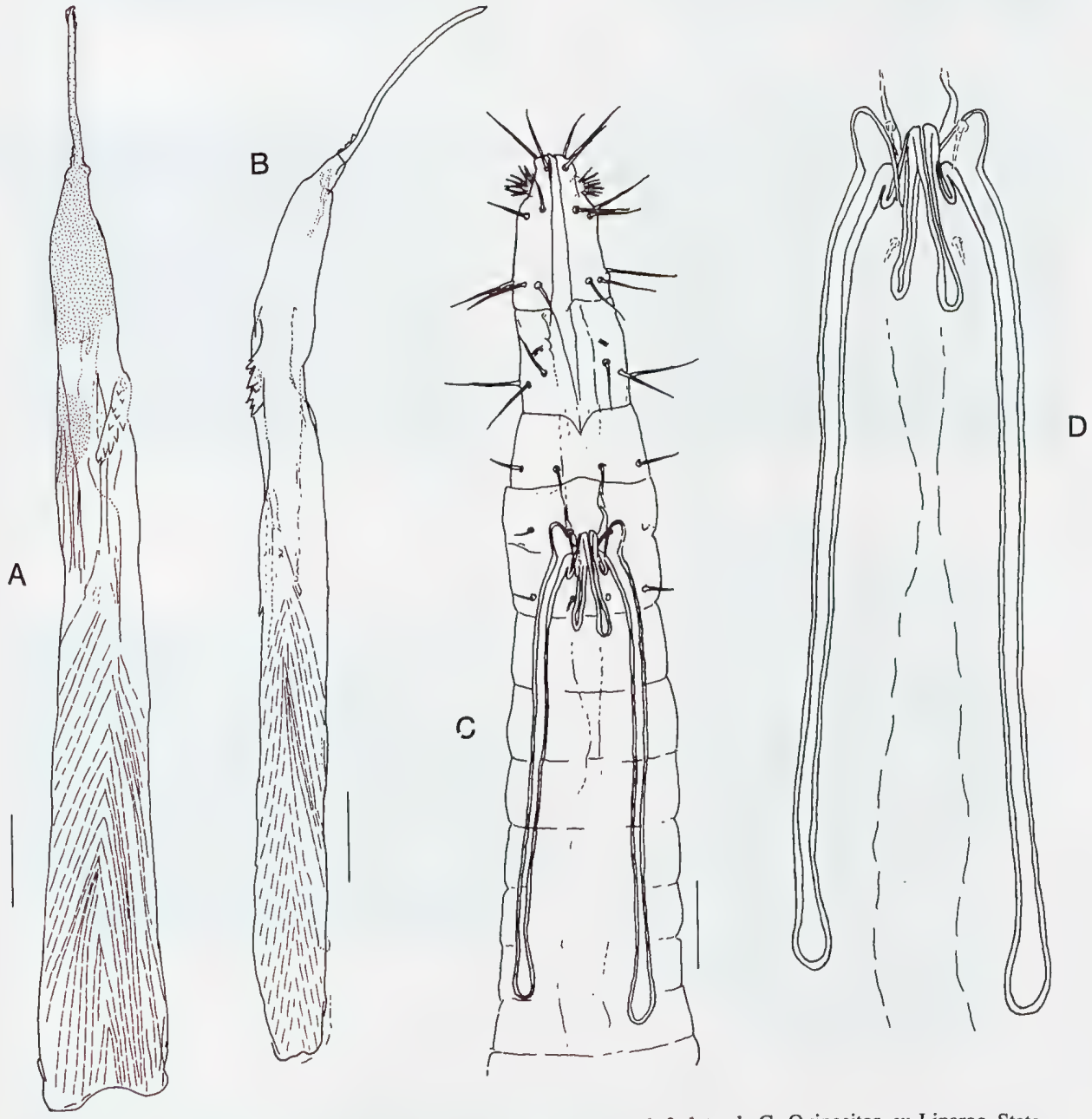


**Fig.17.** *Ballarra molaris* n.sp. A,B. Penis *ex* Beelbangera, ventral & lateral; C. Ovipositor *ex* Liparoo State Forest; D. Detail of seminal receptacles. Scale bars 0.1 mm.

**Description. Males.** *Body.* BL 1.26, CW 0.82. Dorsal pattern on abdomen similar to *B. drosera* with dark brown segmental bars broken by a mesial silvery patch. Eyemound large, unarmed, interocular groove moderately deep; eyes large, situated high on eyemound and directed up at angle of about 30°. Venter mostly pale.

*Spiracle.* Length 0.070, width 0.010. Spines on anterior wall much more numerous and rounder in cross-section than in *B. drosera*; greater tendency for spines to develop on posterior wall. Integument anterior to spiracle with a very narrow zone of sharp micro-ornamentation, posterior to spiracle with numerous closely spaced rows of sharp micro-ornamentation replaced more posteriorly by linguoform micro-ornamentation.

*Chelicerae.* Second segment dorsally with setae but without small denticles; teeth subequal. CSL 0.68.

*Pedipalps.* Very attenuated. Tarsus long, curved dorsad; plumose setae extend to extreme tip, sensory setae and non-socketed setae very few and at extreme tip; claw lacking. Lengths (femur-tarsus) 1.33, 1.02, 0.35, 0.75; ratio patella to tibia 2.91, patella to tarsus 1.36.

*Legs.* Dark brown. Femora lack pseudoarticulations. Tarsi distally with several short articles. Tarsal formula: 30,28,54,-. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 1.48 | 3.19 | 1.60 | 2.64 |
| Tibia | 1.30 | 3.05 | 1.27 | 1.91 |

*Genitalia.* PL 0.086; ratio shaft:glans:stylus 0.59:0.26:0.15; glans long and thin, distally reflexed dorsad. Barbed process oriented at about 25° to shaft axis; barbs moderately numerous (21); basilateral flanges broad, basiventral flanges strong.

**Description. Females.** Similar to male except in the following: appendages relatively longer. Tarsal formula: 26,27,-,28. Key measurements: BL distorted, CTW 0.78, CSL 0.80, PFL 1.75, leg II missing.

*Genitalia.* Lateral seminal receptacles penetrate 4 ovipositor segments, dorsal and ventral 2 segments.

**Variation.** Body of Reabold Hill specimens more extensively pigmented.

**Comments.** This species does not fit easily into *Ballarra* because of the more plesiomorphic condition of: stylus and seminal receptacle length, plume brush on

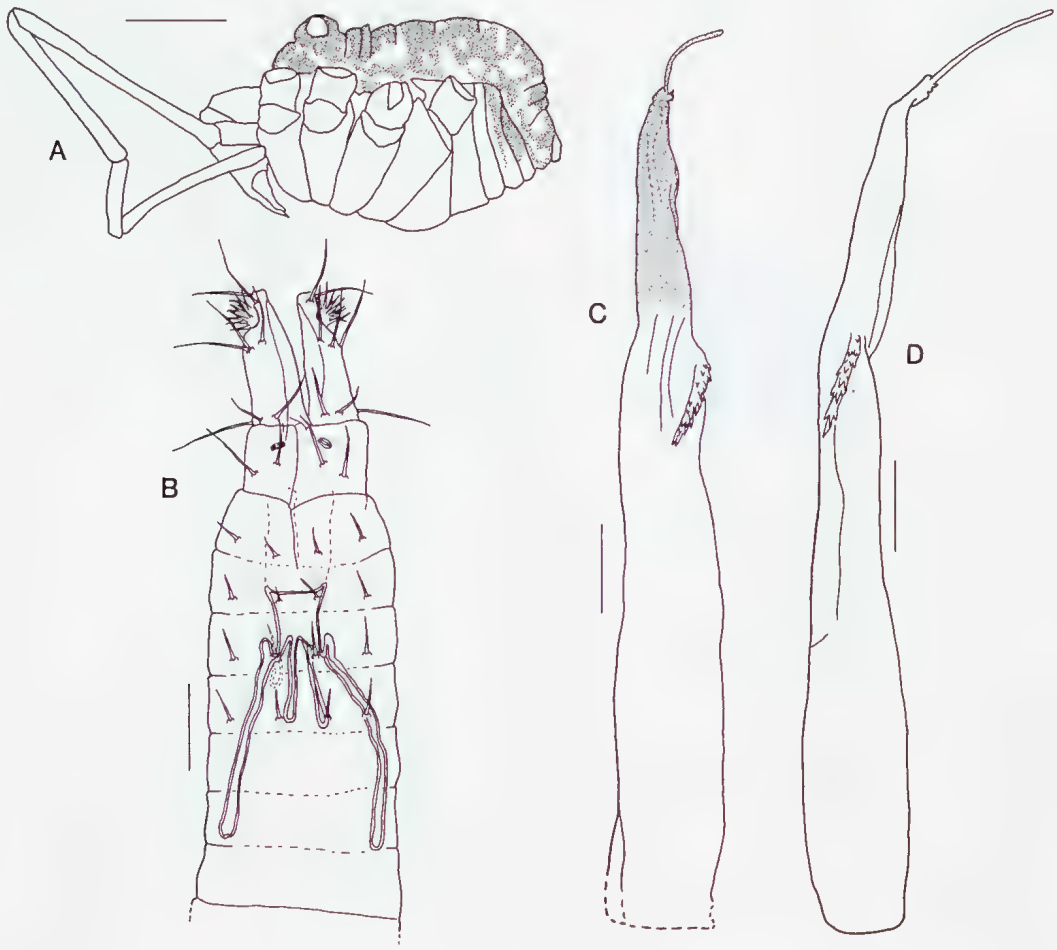


**Fig.18.** *Ballarra longipalpus* n.sp. A. Body of male, lateral; B. Ovipositor, ventral (distal part); C,D. Penis, ventral & lateral. B-D *ex* Reybold Hill. Scale bars: A = 0.5 mm; others 0.1 mm.

each seta, and lack of pseudosegmentation in femur II. It differs from *Plesioballarra*, however, in the form of the pedipalp, and from *Arrallaba* in the form of the penis. We have avoided creating a monotypic genus for this species; it is placed in *Ballarra* rather than *Plesioballarra* because of the seemingly plesiomorphous

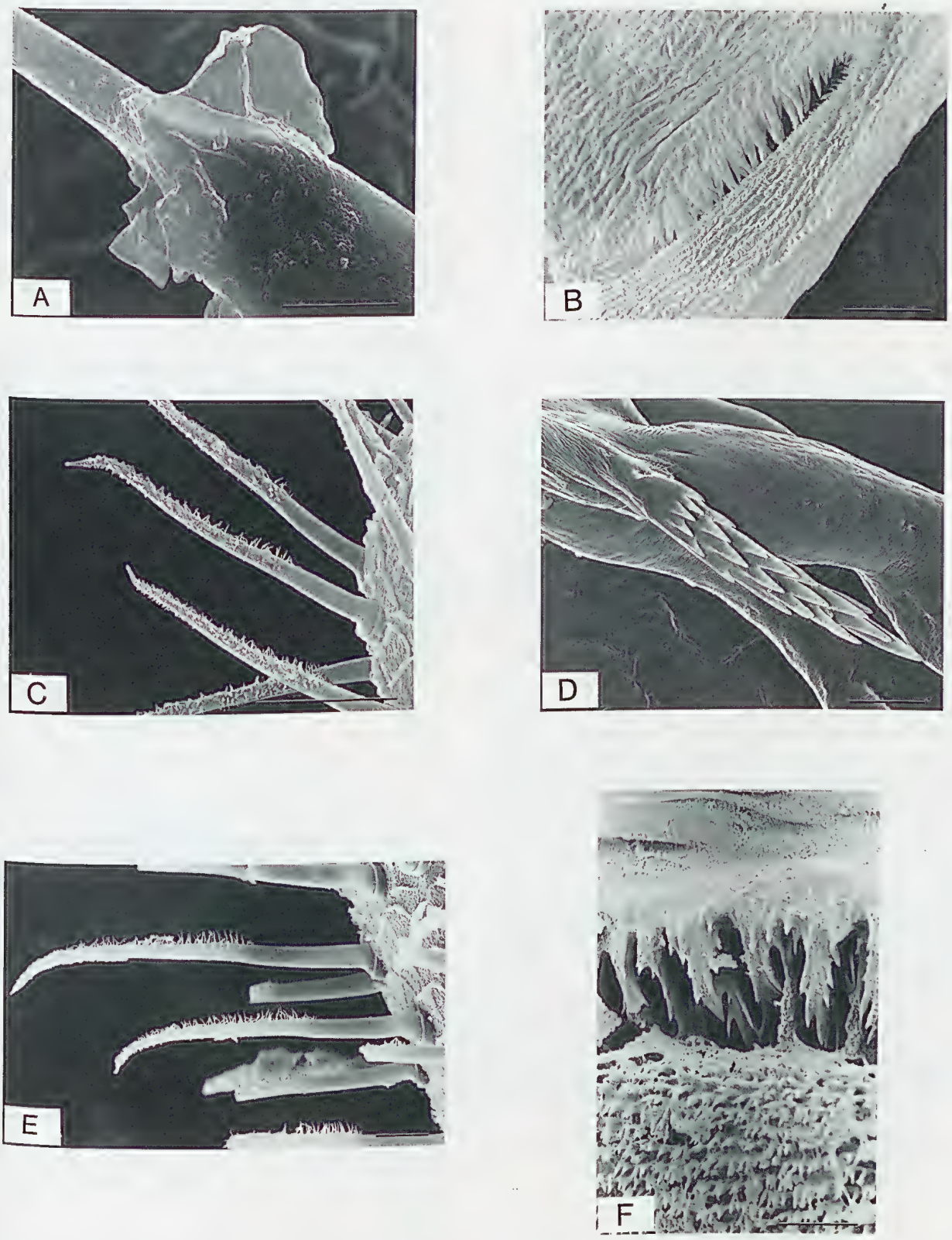


**Fig.19.** Ballarrinae. A-D. *Ballarra longipalpus* n.sp., *ex* Reabold Hill; E,F. *Arrallaba spheniscus* n.sp. A. Base of stylus, ventral (right side damaged); B. Spiracle; C,E. Plumose setae on pedipalp; D. Barbed process of penis, ventral; F. Detail of spiracle spines. Scale bars: A,D,E = 10 μm; B,C,F = 20 μm.

nature of most similarities with the latter genus and because of the weight we attach to similarities in pedipalp structure. The juveniles collected in the Porongorups National Park are tentatively assigned to *B. longipalpus*.

**Etymology.** The specific epithet refers to the extremely long pedipalps.

**Natural history.** Collections from April-July contain immatures, those in August and September adults.

**Distribution.** Perth region, and possibly the Porongorups Range near Albany, Western Australia.

### *Plesioballarra* n.gen.

**Type species.** *Plesioballarra crinis* n.sp., by original designation.

**Diagnosis.** Dorsum lacking prominent heavily pigmented mesial stripe, pedipalp tibia about 0.66 patella length, tarsus not concave dorsad, longer than patella, plumose setae not extending to distal tip but replaced subdistally by prominent zone of sensory and non-socketed setae, plumes extend down most of setal length; stylus about 0.5 glans, barbed process much shorter than glans.

**Description.** Body small, integument soft; eyemound large, interocular groove prominent; plumose setae on pedipalp with plumes along most of setal length; pedipalp patella longer than tibia but shorter than tarsus, tibia about 0.5 patella length; tarsus not curved dorsad, plumose setae not extending to tip of tarsus, non-socketed setae forming a complete subdistal ring, claw easily seen at X12 magnification; all femora lack pseudoarticulations, latter present in tibia II and metatarsi; stylus of penis shorter than glans, basilateral flanges very broad, basiventral flanges well developed; barbed process much shorter than glans; lateral seminal receptacles penetrate 6 ovipositor segments, dorsal and ventral 2 segments, 1:1-1:1 slit sensilla on second furcal segment.

**Etymology.** This genus has several seeming plesiomorphies associated with the pedipalp (cladistic analysis resolves them as reversals). Gender is feminine.

**Distribution.** Border ranges of eastern New South Wales to Queensland.

### *Plesioballarra crinis* n.sp.

Figs 20-21

**Type material.** HOLOTYPE: QM 15521, Bald Mountain area, via Emu Vale, Qld, 28°14'S 152°25'E, T. Weir, Feb. 1970; 1M. PARATYPES: QM 15522, 1150-1300m, B.K. Cantrell, 27-31 Jan. 1972; 1F. QM, same data; 1M,8F. UQ, T. Weir, Feb. 1970; 1M. UQ, 1000-1500m, B.K. Cantrell, 17-22 May 1969; 1F. AM KS 20144, same data; 1M. AM KS20143, T. Weir, Feb. 1970; 2M,1J. UQ, 1000-1300 m, B.K. Cantrell, 22-27 Jan. 1971; 1M. UQ, B.K. Cantrell, 26-30 Jan. 1973; 1M,2F. Lamington National Park, 28°15'S 153°10'E: QM, B.K. Cantrell, 4 Jan. 1968; 1M,2F. UQ, same data; 1M. ANIC, Wiangaree State Forest, NSW, 28°22'S 153°05'E, 1050 m, T. Weir & A. Calder, 10-12 Feb. 1983; 1F.

**Other immature material examined.** Mount Bithongabel, Lamington National Park, Qld, 28°15'S 153°09'E: QM, stick brushing berlesate no. 203, rainforest, G.B. Monteith, 8 Oct. 1979; 1J. QM, sweeping, V.E. Davies & R. Raven, 16 Nov. 1977; 1J.

**Diagnosis.** Interocular groove deep. Pedipalp tarsal claw prominent; plumose setae not extending to tip of tarsus but replaced by subdistal band of non-socketed setae and terminal tuft of sensory setae; plumes extend along most of setal length. Leg tarsi distally with numerous short articles. Penis stylus much shorter than glans; basal flanges pointed distad; barbed process at 45° to shaft axis.

**Description. Males.** *Body.* BL 2.23, CTW 1.21. Dorsal colour pattern (old specimen in alcohol) as figured, dark brown with yellow-brown and silvery patches; large silver-gold saddle-like patch posterior to metapeltidium; anterior to eyemound pale. Eyemound large, deeply canaliculate, with a few dorsal spicules, pale except for eye pigment. Eyes large, directed up at about 30° to horizontal. Venter pale but abdomen pigmented at margins.

*Spiracle.* Length 0.13, width 0.04. Spines on anterior wall extremely dense, attenuated, with multiple terminations; those on posterior wall dense but less developed. Spiracle ringed by broad zone of closely spaced rows of sharp micro-ornamentation, more posteriorly with rows of widely spaced linguoform-globular papillae.

*Chelicerae.* Basal segment dorsally with large pale patch. CSL 0.73.

*Pedipalps.* Stout. Large pale band about half way along femur, patella and tarsus. Dorsal angle between patella and tibia only slightly less than 180°. Tarsus not curved dorsad. Plumes extend along most of setal length. Plumose setae on tarsus replaced subterminally by zone of non-socketed setae and terminally by tuft of socketed and non-socketed setae. Claw prominent compared with other Neopilionidae. Lengths (femur-tarsus) 1.30, 0.78, 0.52, 0.93; ratios patella to tibia 1.50, patella to tarsus 0.84.

*Legs.* Pale band about half way along femora and tibiae; articulations and pseudoarticulations pale. Femur II without, tibia II with pseudoarticulations; tarsal articulations often swollen; tarsi strongly prehensile with numerous short articles. Tarsal formula: 29,52,32,33.

Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 2.53 | 5.25 | 2.41 | 3.77 |
| Tibia | 1.99 | 4.84 | 1.88 | 2.69 |

*Genitalia.* PL 1.24; stylus relatively short, glans elongate, ratio shaft:glans:stylus 0.64:0.23:0.13. Barbed process oriented at about 45° to penis axis; barbs numerous (26 and 28, n = 2). Basilateral flanges of stylus strongly

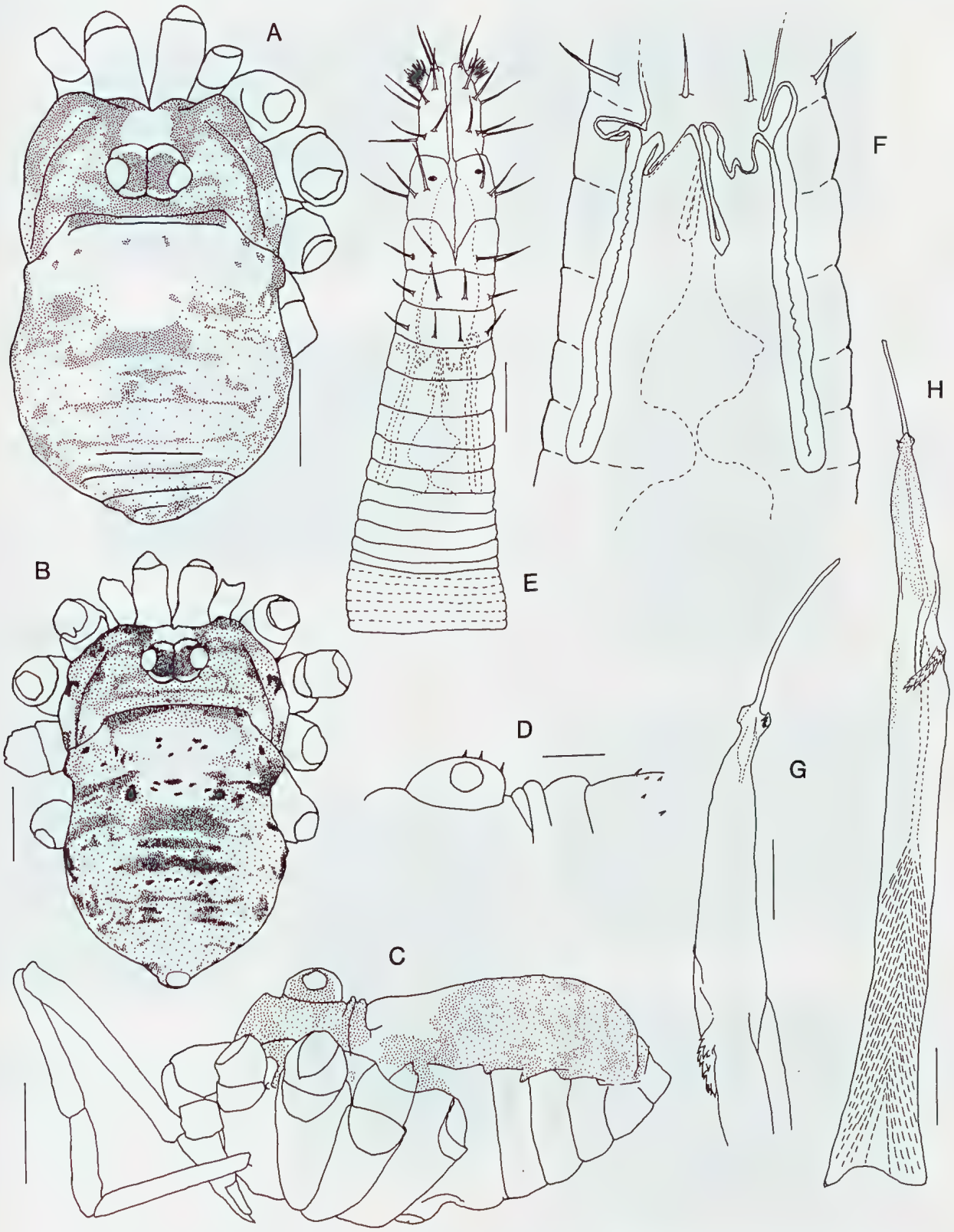


**Fig.20.** *Plesioballarra crinis* n.sp. A,C. Body of male *ex* Bald Mountain, dorsal & lateral; B. Body of male *ex* Lamington Plateau, dorsal; D. Detail of eyemound, lateral; E. Ovipositor, dorsal; F. Detail of seminal receptacles; G,H. Penis, lateral & ventral. Scale bars: A-D = 0.5 mm; E-H = 0.1 mm.

pointed; basiventral flanges strongly developed.

**Description. Females.** Similar to males except in the following: body slightly larger, pedipalp and legs shorter. Key measurements: BL 2.43, CTW 1.40, CSL 0.83, PFL 1.08, LFL 3.33, LTL 3.42 Tarsal formula: 30,55,31,31.

*Genitalia.* Lateral spermathecae penetrate 6 ovipositor

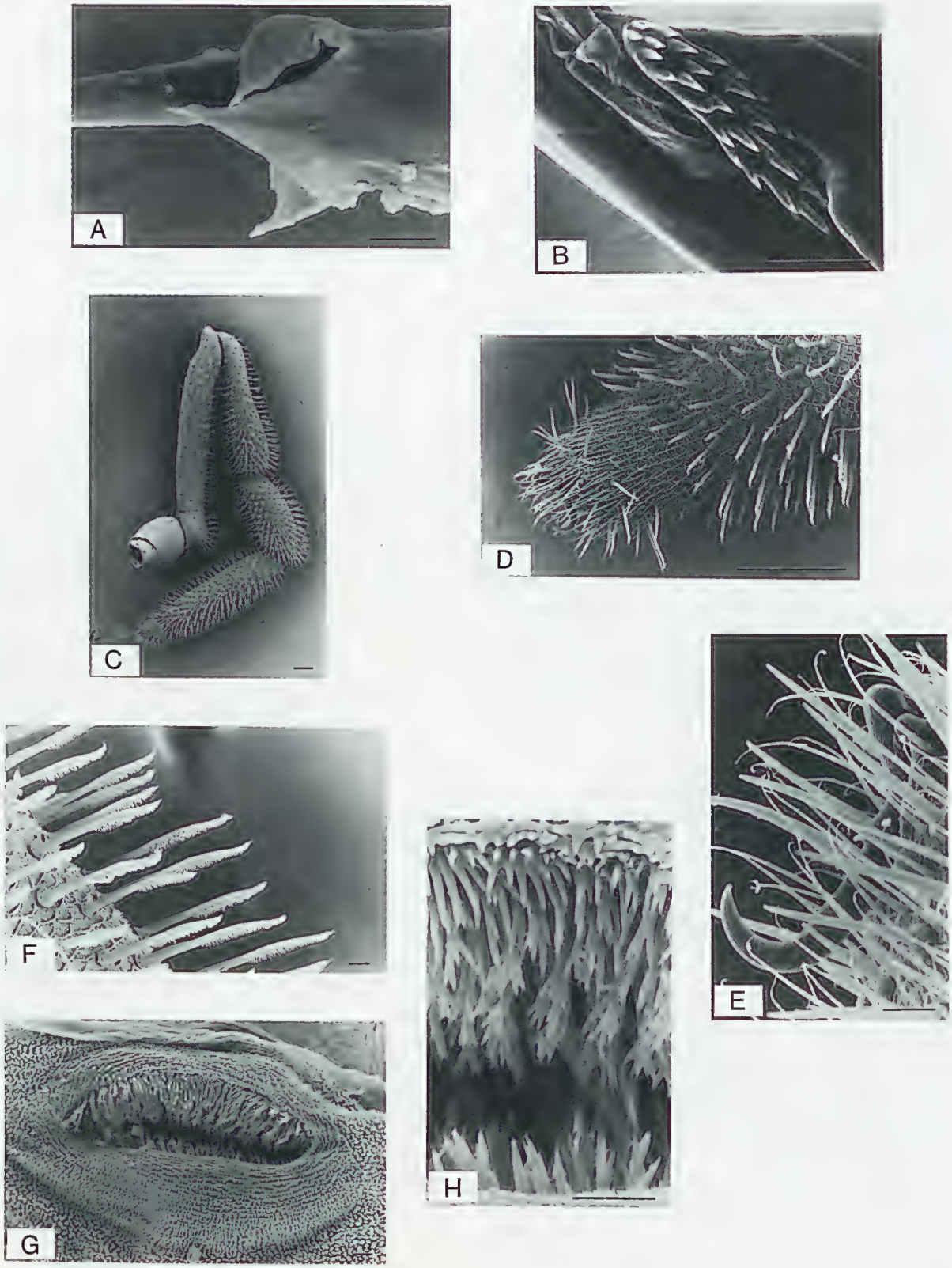


**Fig.21.** *Plesioballarra crinis* n.sp. A. Base of stylus, ventrolateral; B. Barbed process of penis, ventral; C. Pediplap, retrolateral; D. Detail of pedipalp tarsal tip; E. Detail of pedipalp tarsal claw; F. Plumose setae on pedipalp; G. Spiracle; H. Detail of spiracle spines. Scale bars: A,E-H = 10 µm; C,D = 100 µm.

segments, dorsal and ventral 2 segments.

**Comments.** The structure of the pedipalp distinguishes this species from all other Ballarrinae. *Plesioballarra crinis* resembles the Western Australian *B. longipalpus* n.sp., in the prominent interocular groove, the absence of pseudosegmentation in the femur of leg II, the relatively short stylus with prominent basal flanges, the relatively short seminal receptacles and the form of the plumose setae.

**Etymology.** The specific epithet is a Latin noun meaning 'tuft of hair' and refers to the remnant tuft-like cluster of sensory setae at the tip of the pedipalp tarsus.

**Natural history.** Juveniles have been collected in spring-summer, adults January to May.

**Distribution.** Border Ranges of south-eastern Queensland and north-eastern New South Wales.

### *Arrallaba* n.gen.

**Type species.** *Arrallaba spheniscus* n.sp., by original designation.

**Diagnosis.** Abdomen with prominent virtually continuous heavily pigmented mediodorsal stripe; pedipalp tibia less than 0.5 patella length, tarsus concave dorsad and shorter than patella, plumes extend along most of setal length; stylus of penis extremely short and twisted, barbed process longer than glans, flattened.

**Description.** Body large for Ballarrinae, elongate; integument soft; abdomen dorsally with prominent virtually continuous median stripe; plumose setae on pedipalp with plumes along most of setal length; pedipalp patella longer than tibia and tarsus, tibia less than 0.5 patella; tarsus curved distad, plumose setae extend to tip of tarsus, sensory and non-socketed setae confined to extreme tip, latter not forming a subdistal ring, claw absent; leg femora without pseudoarticulations, latter in tibia II and metatarsi; stylus of penis extremely short, coiled; barbed process greatly enlarged, longer than glans, flattened; lateral spermathecae penetrating 3 ovipositor segments, dorsal and ventral penetrating 2 (perhaps 3) segments; sexual dimorphism slight.

**Etymology.** A latinised backward spelling of the new genus *Ballarra* emphasising the opposite state of many characters. Gender is feminine.

**Distribution.** "Australian Alps" region of south-east mainland Australia.

### *Arrallaba spheniscus* n.sp.

Figs 19E-F, 22

**Type material.** HOLOTYPE: ANIC, 1km north of Mount Gingera, Brindabella Range, ACT, 35°35'S 148°46'E, stop 18, in gutter trap, D.C.F. Rentz & J. Balderson, 21 Feb. - 10 May 1979; 1F. PARATYPES: ANIC, same data; 1F. AM KS 19121, same data; 1F. ANIC, South Ramshead, Kosciusko National Park, NSW, 36°28'S 148°20'E, altitude 1750 m, pit trap, K. Green, summer-autumn 1982-1983; 1F. ANIC, same data, 1M.

**Diagnosis.** See generic diagnosis.

**Description. Females.** *Body.* Elongate, BL 4.07, CTW 1.66. Dorsal pattern as figured, pigmented areas maroon-brown; prominent median stripe, wider at metapeltidium and broken only posteriorly by thin intersegmental lighter patches; median stripe accentuated by flanking pale stripe; dorsum heavily pigmented laterally. Sternites heavily pigmented except at sutures. Anterior margin strongly indented above chelicerae. Eyemound black, situated about 0.7 its length behind anterior margin, moderately large and armed with a few small spicules; interocular groove shallow.

*Spiracle.* Elongate, length 0.130, width 0.020. Spines on anterior wall complex, somewhat flattened in section, with multiple terminations; enlarged spines on posterior wall absent. Integument anterior to spiracle smooth; posterior to spiracle with closely spaced rows of sharp micro-ornamentation.

*Chelicerae.* Elongate and slender. Each finger with moderately enlarged proximal tooth and row of small subequal teeth. CSL 1.36.

*Pedipalps.* Relatively shorter than in *Ballarra.* Tarsus short, curved dorsad but not strongly; non-socketed setae in small terminal group; claw lacking. Lengths (femur-tarsus) 1.46, 1.24, 0,50, 0.89; ratios patella to tibia 2.48, patella to tarsus 1.39.

*Legs.* Relatively short and stout. Distal half of tarsi finely divided into many short articles, strongly prehensile. Tarsal formula: 25,46,24,29. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 1.78 | 2.76 | 1.99 | 2.49 |
| Tibia | 1.54 | 2.64 | 1.56 | 2.19 |

*Genitalia.* Terminal portion of ovipositor as figured; lateral spermathecae penetrate 3 segments, dorsal and ventral penetrate 2 (perhaps 3) segments.

**Description. Male** (badly damaged). Similar to female except in the following: second segment of chelicera slightly more robust; pedipalp tarsus relatively shorter; legs relatively longer. Tarsal formula: 25,43,28, 31. Measurements: body distorted, CSL 1.34, pedipalp lengths (femur-tarsus) 1.20, 1.02, 0.40, 0.85, ratios patella to tibia 2.55, patella to tarsus 1.20.

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | 2.12 | 3.76 | 2.02 | 3.11 |
| Tibia | 1.79 | 3.43 | 1.83 | 2.86 |

*Genitalia.* PL 0.847; shaft relatively long and very broad, glans relatively short and very narrow, stylus extremely short and tightly curved, ratio shaft:glans: stylus 0.78:0.20:0.03; barbed process greatly enlarged,

longer than glans, flattened in section, curved distally across midventral line of shaft; barbs mostly on margin of process closest to mid-line of shaft.

**Comments.** The structure of the penis distinguishes this species from all other Ballarrinae. The species resembles *B. clancyi* and *B. molaris* in loss of non-socketed setae and tarsal claw from the pedipalp, and also the relatively short legs and finely divided tarsus of the latter.

**Etymology.** The specific epithet refers to the shape and positioning of the barbed process which calls to mind a penguin's wing; *Spheniscus* being the type genus of the penguin family.

**Natural history.** Despite a seasonal pitfall trapping project in the Mount Kosciusko region which extended over two years and a gutter trapping project in the Brindabella Ranges, the few individuals were trapped only in summer-autumn (Dr Ken Green, personal communication).

**Distribution.** "Australian Alps" of south-eastern mainland Australia, from Brindabella Range to Mount Kosciusko area.

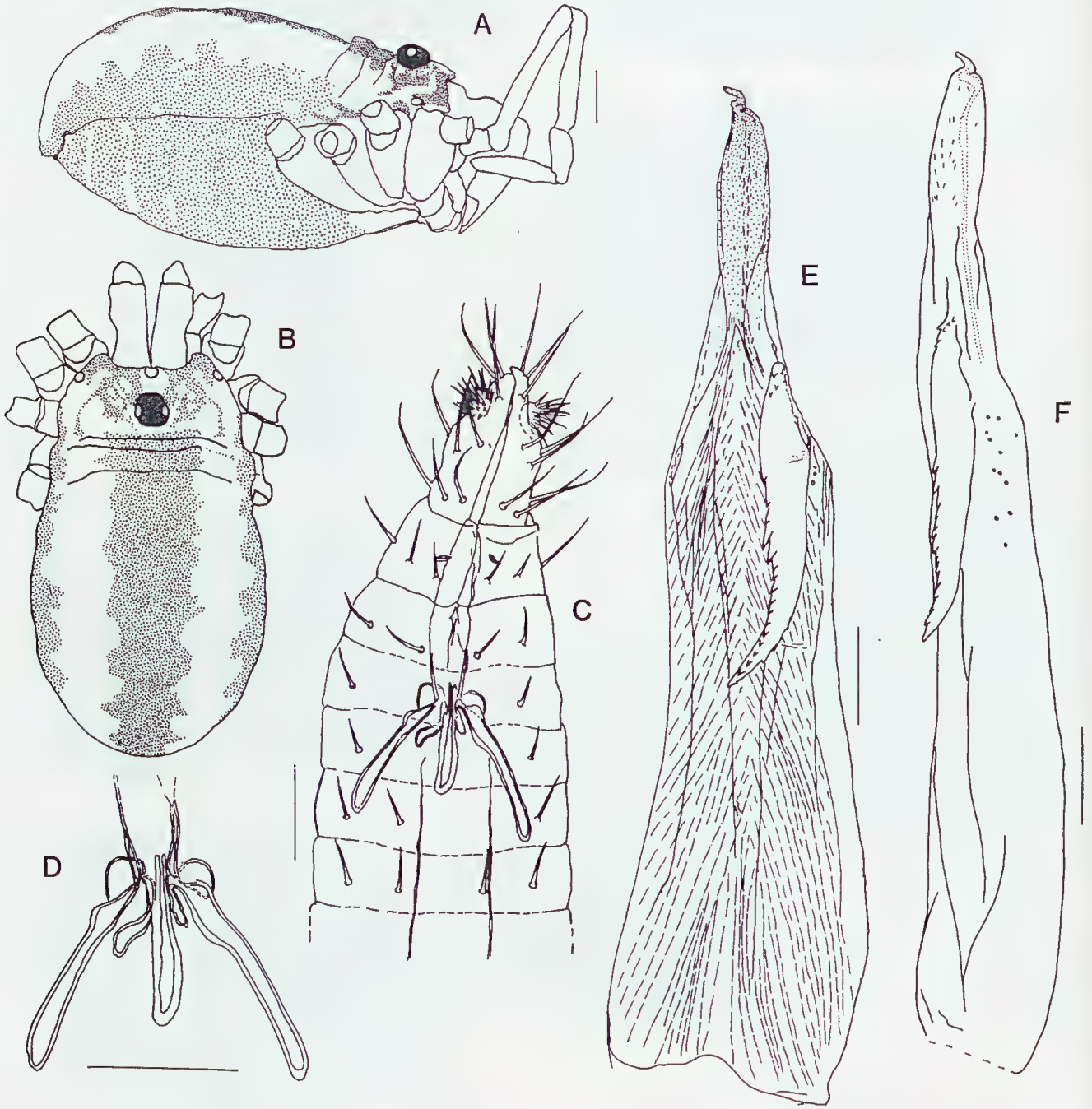


**Fig.22.** *Arrallaba spheniscus* n.sp. A,B. Body of female, lateral & dorsal. C. Ovipositor, dorsal (distal part); D. Detail of seminal receptacles; E,F. Penis, ventral & lateral. Scale bars: A,B = 0.5 mm; others 0.1 mm.

### *Vibone* Kauri, 1961

*Vibone* Kauri, 1961: 143.–Silhavy, 1970: 171, 174.–Lawrence, 1981: 17.–Shear, 1982: 110.–Martens, 1978: 229.

**Type species.** *Vibone vetusta* Kauri, 1961, by original designation.

**Diagnosis.** As far as can be determined from Kauri's drawings and excellent description of the female holotype of *V. vetusta*, *Vibone* is similar to *Ballarra* females except in having an ovipositor corpus with only 2 segments, 2 seminal receptacles, a tibia greater than 0.5 length of patella and more pronounced pseudo-articulatory nodules on all leg femora.

The seminal receptacles are in the superior part of the internal vagina, each consisting of an elongated loop.

As in some other Ballarrinae, the palpal claw is lacking.

**Description.** See Kauri (1961). The only specimen, the female holotype, has apparently been lost.

**Natural history.** The only known specimen, a mature female, was collected on 18 December at 730 m elevation from moist ground litter in a humid valley with abundant undisturbed native vegetation (trees and bushes).

**Distribution.** Known only from the type locality, Table Mountain, Republic of South Africa (Fig.1).

### *Americovibone* n.gen.

**Type species.** *Americovibone lanfrancoae* n.sp., by original designation.

**Diagnosis.** Chelicera with ventral spur on the basal segment; pseudosegments present in the palpal segments of the female and at least leg femora and tibiae II-IV of both sexes; pedipalp patella longer than tibia or tarsus, palpal claw absent; leg claws with lateral teeth on each side; penis lacking barbed process, ovipositor with 2 spermathecae.

**Description.** Minute harvestmen with relatively long legs. Eye mound and body unarmed, smooth. Chelicerae with spur on basal segment. Female pedipalp with pseudosegments in femur and patella; pedipalp patella longer than tibia and tarsus, tarsus concave dorsad along its length in female and curved in opposite sense in male, tarsal claw and non-socketed setae absent, plumose setae extend to the tarsal tip, plumes not clearly bifurcate. Leg femora and tibiae with pseudosegments, claws with lateral branches on each side. Penis without bristle groups or processes. Ovipositor corpus of more than 2 segments, 2 spermathecae.

**Etymology.** The generic name is a contraction of "American *Vibone*" and is feminine in gender.

**Distribution.** Known only from southern Chile (Fig.1).

### *Americovibone lanfrancoae* n.sp.

Figs 23-24

**Type material.** Chile, Peninsula de Brunswick, Magallanes: HOLOTYPE: MNHN, Reserva Nacional Magallanes, 8 km west of Punta Arenas, J. Peterson C., 24 Feb.-23 Mar. 1978, Trampa Barber no. 13-2nd Trampeo; 1M. PARATYPE: AM KS20142, same data, Trampa Barber no. 11-1st Trampeo; 1F.

**Description. Male.** *Body.* BL 0.86, CTW 0.64. Dorsum light brown on lateral edges of cephalothorax and abdomen, with remainder of cephalothorax brown and eye mound dark brown; abdomen with three indistinct transverse bands of dark brown, middle band broken in centre (pattern unclear as abdomen is shrivelled); venter light tan to yellowish. Integument thin, smooth except for legs which are subimbricate to rugose in appearance. Few minute setae on coxae and sternites. Eyemound smooth, unarmed, wider than long, removed from edge of cephalothorax by less than mound length, not canaliculate. Anterior edge of cephalothorax impressed in front of eyemound. Spiracles undetected (due to small size and dark pigmentation).

*Chelicerae.* Brown with black denticles on jaws, basal portion of first segment whitish. Relatively short and slender; basal segment with retrolateral row of 4 or 5 slit sensilla; unarmed except for few minute setae and mesal series of bi- and tri-pointed scales; ventral spur on basal segment; CSL 0.44.

*Pedipalps.* Brown, bases of femur and trochanter whitish. Femur with distodorsal slit sensillum. Femur, tibiae, patellae, and tarsus with plumose setae of sub-equal size, tarsus with greatest density; plumes restricted to the setal tip; integument smooth, lacking pseudosegments. Lengths (femur-tarsus) 1.35, 0.95, 0.47, 0.68; ratios patella to tibia 2.02, patella to tarsus 1.40. Palp not examined with SEM.

*Legs.* Brown, white ring on last article of metatarsus, base of femur whitish. Long and slender; femora I-IV with numerous pseudosegments (-,13,6,7-9), distal two especially noticeable and enlarged as nodules; tibiae through tarsi also with pseudosegments. Tarsal formula: -,-,30,30-34. Measurements:

| Leg | I | II | III | IV |
|---|---|---|---|---|
| Femur | – | 2.88 | 1.77 | 2.51 |
| Tibia | – | – | 1.54 | 2.40 |

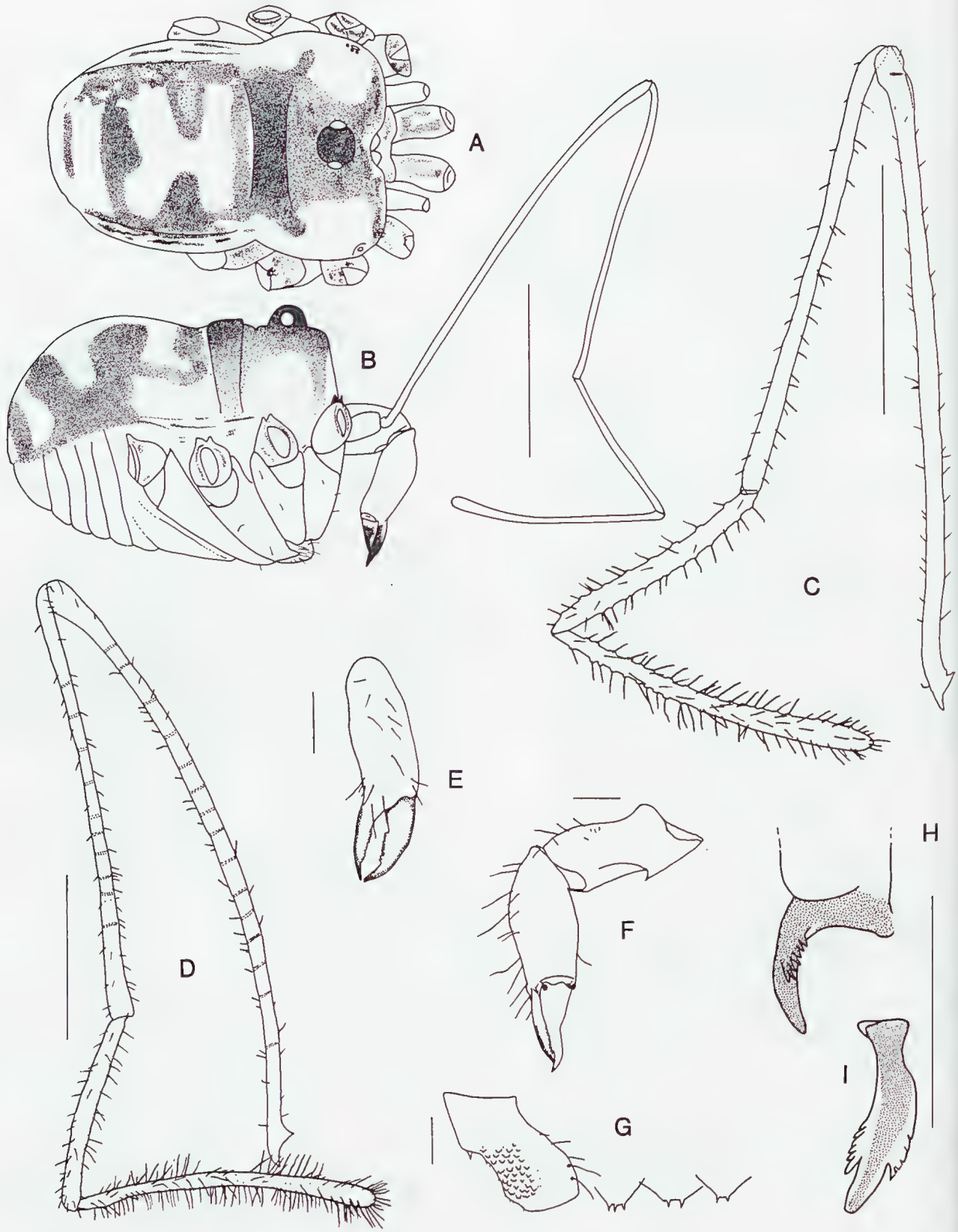


**Fig.23.** *Americovibone lanfrancoae* n.sp. A,B Body of male, dorsal & lateral (slightly reconstructed from distorted specimen); C,D. Pedipalp, male & female; E. Male chelicera, second segment, dorsal; F. Male chelicera, retrolateral; G. Basal segment, prolateral with detail of bi- and tri-pointed scales; H,I. Tarsal claw of leg I, lateral & dorsal. Scale bars: A-D = 0.5 mm; others 0.1 mm.

*Genitalia.* Glans shorter and more slender than in *Ballarra*, stylus with a contorted loop arising on the dorsolateral end; shaft compressed dorsoventrally on lateral sides.

**Description. Female.** Similar to the male except in the following; pedipalp tarsus concave dorsad, more setose; plumes extend down most of setal length; pedipalp femur and patella with pseudosegments, 16:17, 10:11 respectively.

**SEM of the female palp.** Plumose setae extend to distal tip of tarsus; plumes extend along most of setal length, not obviously bifurcate; sensory setae very few, restricted to tarsal tip; non-socketed setae and claw lacking.

**Measurements.** Body distorted, CSL 0.46, pedipalp lengths femur-tarsus 1.97, 1.37, 0.63, 0.98, ratio patella to tibia 2.17, patella to tarsus 1.40. Legs missing.

**Ovipositor.** With 3-segmented furca, plus 8 rings; slit sensilla of furca are replaced by small ridges on each side; paired seminal receptacles within third and fourth rings from furca; setae present on furca and distal 7 rings; seminal receptacles each consisting of 1 short single loop with 2 lateral extensions.

**Comments.** The spicules (pointed scales) on the chelicerae are present on both sexes. It is possible they are used in sound production. The spicules resemble those found on some members of the Schizomida, which are also found on both sexes and have been questionably proposed as stridulatory structures (Cokendolpher, 1988).

The curious difference between the male and female in the form of the pedipalp tarsus and setal plumes suggests the possibility of two sympatric species. A larger series is required to determine this.

**Natural history.** Both known specimens were collected in Barber traps set in evergreen coige forest (*Nothofagus betuloides*) at 250 m with a 50° slope and a floor of 5-7 cm of dead leaves. A detailed account of this forest is provided by Dollenz A. (1982).

**Distribution.** Known only from the Peninsula de Brunswick, Patagonia, Chile (Fig.1).

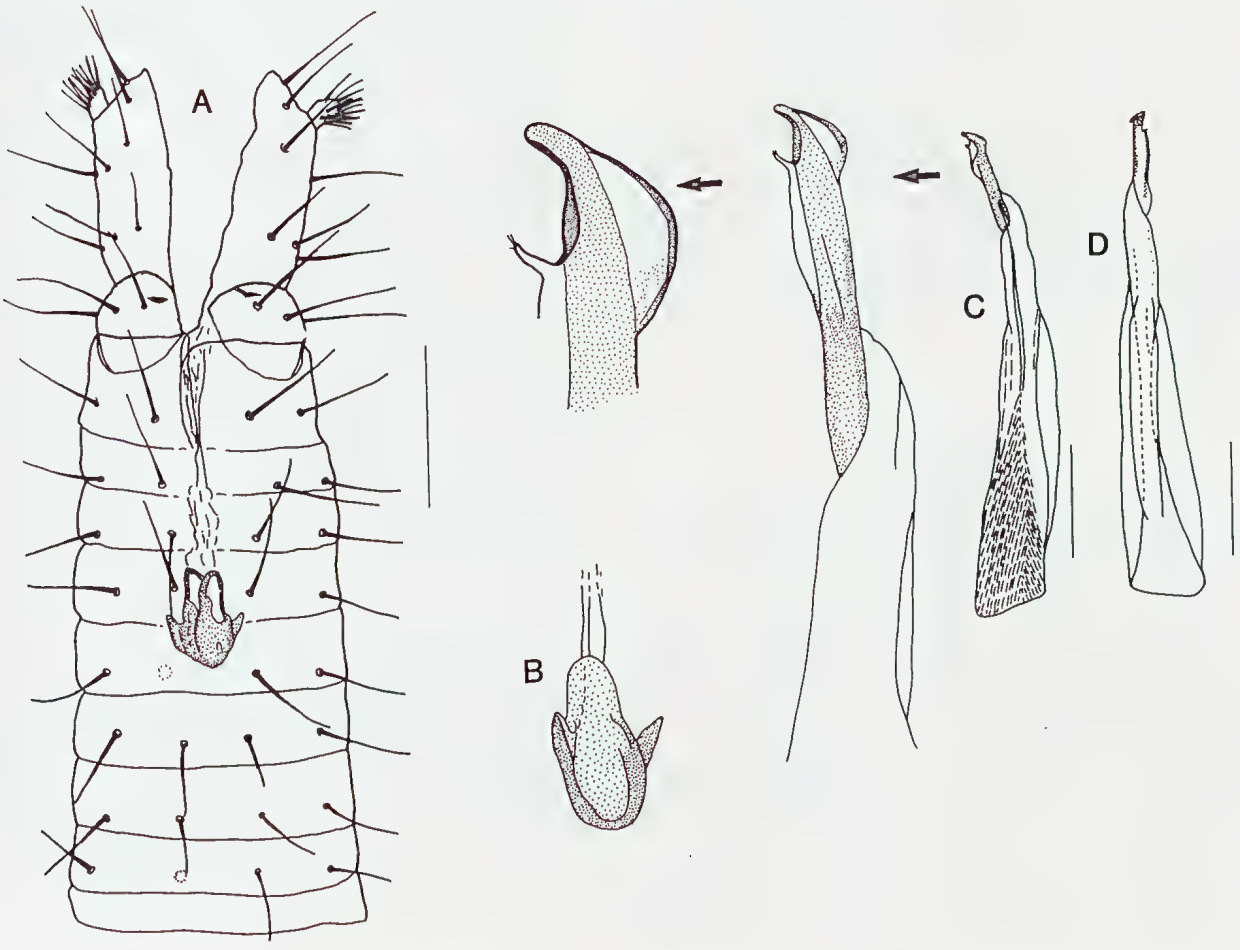


**Fig.24.** *Americovibone lanfrancoae* n.sp. A. Ovipositor, dorsal; B. Detail of seminal receptacle; C. Penis, lateral, with detail of glans and stylus; D. Penis, ventral. Scale bars 0.1 mm.

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## APPENDIX 1

Table 1. Full character matrix used in cladistic analysis of selected Phalangioidea (0 = plesiomorphic, 1 = apomorphic, ? = unknown or not relevant).

| Characters | 1 | 2 | 3 | 4 | 5 | | | | | 10 | | | | | 15 | | | | | 20 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ancestor | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Phalangiidae | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | 0 |
| Gagrellidae | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 | ? | 0 |
| *Megalopsalis* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ? | 0 |
| Some *Pantopsalis* spp. | 0 | 0 | 0 | 1 | ? | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | ? | 0 | 0 | 0 | ? | 0 |
| N.gen. (?Monoscutinae) | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | ? | 0 |
| *Spinicrus nigricans* | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | ? | 0 |
| Enantiobuninae | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | ? | 0 | 0 | 0 | ? | 0 |
| *Neopilio* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | ? | 0 |
| *Americovibone* | 1 | 1 | 1 | ? | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | ? | ? | 1 | 1 | ? | 0 |
| *Plesioballarra* | 1 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Arrallaba* | 1 | 1 | 1 | ? | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 |
| *Ballarra* | 1 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *Vibone* | 1 | 1 | 1 | ? | ? | ? | 1 | 1 | ? | ? | ? | ? | 1 | 0 | ? | ? | 1 | 0 | ? | 1 |

The following protocol was followed:

Analysis 1. Full data set of 20 characters

Analysis 2. Character 8 deleted (Fig.4A)

Analysis 3. Characters 1, 8 and 17 deleted (Fig. 4B).

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# Salticidae (Arachnida: Araneae) of Oriental, Australian and Pacific Regions, V. Genus *Holoplatys* Simon, 1885

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ABSTRACT. The spider genus *Holoplatys* Simon is revised. Its relationships, origin and distribution are discussed. Six species groups based on genitalia and body structure are distinguished and key for their identification in proposed. *Holoplatys caledonica* Berl., *H. urvillei* Dalmas, *H. fractivittata* Sim. and *H. quinquecinqulata* Sim. are excluded from the genus. *Ocrisiona complanata* (L.K.), *O. invenusta* (L.K.) and *O. fusca* (Karsch) are included in *Holoplatys*. A total of 37 species are described and figured, including 31 new species: *bicoloroides, borali, braemarensis, bramptonensis, canberra, chudalupensis, colemani, complanatiformis, daviesae, dejongi, desertina, embolica, grassalis, jardinensis, julimarina, kalgoorlie, kempensis, lhotskyi, mascordi, meda, minuta, oakensis, panthera, pedder, pemberton, rainbowi, queenslandica, semiplanata, strzeleckii, tasmanensis* and *windjanensis*.

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A recent survey of the Australian Salticidae provides the list of 57 genera, most of them endemic (Davies & Zabka, 1989). Seven species are recorded from the genus *Holoplatys* (Simon 1901b, 1909; Dalmas, 1917; Berland, 1932; Koch, 1879), but an examination of type and new material shows that the real number of species is far greater. Thirty one new species are recognised and, in comparison to Bonnet's list (1957), the generic status of four species is altered. *Holoplatys caledonica* Berland, 1932, *H. fractivittata* Simon, 1909 and *H. quinquecinqulata* Simon, 1909 are transferred to new genera (Zabka, in preparation). *Holoplatys urvillei* Dalmas, 1917 should be included in *Trite* Simon. At the same time *Ocrisiona complanata* (L. Koch, 1879), *O. invenusta* (L. Koch, 1879) and *O. fusca* (Karsch, 1878) have been transferred to *Holoplatys*. *Ocrisiona cinerea* (L. Koch, 1879) and *O. liturata* (L. Koch, 1879) probably also belong to *Holoplatys* but as neither adult type specimens nor fresh material of either species are available, they are not included here.

Basically, the type species, *H. planissima* (L. K.) is the only species in the genus to have been studied in any detail (Prószynski, 1984; Davies & Zabka, 1989).

## Material and Methods

The work is based on type specimens from European collections listed by Prószynski (1971) and on new material borrowed from several Australian museums and collected by the author. Twenty two species were described from one sex only and of these 18 were from a single specimen. The full list of collections used is presented below. Means (in brackets) and ranges are given in millimetres. The details of terminology are illustrated in Figure 1. Format of leg spination follows Platnick & Shadab (1975). Dissected epigynes were digested in lactic acid for 10 to 30 minutes or in 10% KOH for 12 to 48 hours at room temperature, rinsed in distilled water, stained in ethanol solution of chlorazol black E under control and then mounted in glycerin. The drawings were made using grid system. New specific names are derived from localities or, in other cases, their etymology is explained.

Close affinities within the genus and very fine specific differences do not provide enough clearly defined characters for a species identification key to be constructed. Only a key for the species groups is proposed.

Collections studied include: AMS - Australian Museum, Sydney; ANIC - Australian National Insect Collection CSIRO, Canberra; MNHN - Museum National d'Histoire Naturelle, Paris; QMB - Queensland Museum, Brisbane; SAMA - South Australian Museum, Adelaide; TMH - Tasmanian Museum and Art Gallery, Hobart; WAMP - Western Australian Museum, Perth; ZMB - Zoologisches Museum der Humboldt-Universität, Berlin; ZMH - Zoologisches Institut und Zoologisches Museum, Universität Hamburg. Abbreviations used are: AEW - anterior eyes width, ag - accessory gland, AL - abdomen length, cd - cephalic depression, cf - cymbial flange, CL - cephalothorax length, CW - cephalothorax width, da - dorsal tibial apophysis, e - embolus, EFL - eye field length, ep - epigynal pocket, fd - fertilisation duct, id - insemination duct, m - metatarsus, p - prolateral spines, PEW - posterior eyes width, r - retrolateral spines, s - spermatheca, sc - abdominal scutum, sd - seminal duct, t - tibia, tg - tegulum, ta - lateral tibial apophysis.

## Taxonomic Survey

### *Holoplatys* Simon

*Marptusa* [part] L. Koch, 1879: 1100.
*Holoplatys* Simon, 1885: 88.
*Ocrisina* [part] Simon, 1901: 595, 602, 604, 608.

**Type species.** *Marptusa planissima* L. Koch, 1879, by monotypy.

**Diagnosis.** Genitalia structure, very flat body and cephalic depressions between posterior lateral eyes separate *Holoplatys* from other Australian genera. Tibial spines on first and second legs absent in most species.

**Description** (Fig.1). Tiny to large spiders, ranging from 2 to 11 mm in length. Body flat and narrow. Thoracic part of cephalothorax distinctly longer (up to

72% of total length) than cephalic part. Fovea displaced backwards, indistinct or not visible. Most species with 2 shallow cephalic depressions. Abdomen elongate, often with anterior scutum - better marked in males. Clypeus very narrow, in some species with fringe of short white hairs. Chelicerae small or very small, displaced backwards (Fig.1B), of unident pattern, with 2 promarginal teeth and 1 retromarginal tooth, the last sometimes missing. Maxillae and labium elongated. Legs I long and strong, especially in *planissima* group, their tibiae and metatarsi often cone-shaped, patellae and tibiae sometimes fringed. Legs III the shortest, IV the longest or as long as I. Spines on tibia and metatarsus I and II usually (but not always) absent.

On the basis of general body form, colour pattern and genitalic structure six species groups are proposed: *complanata, planissima, grassalis, panthera, bicolor* and *invenusta*. Palpal organ (Figs 1C-E, 2A-T) with sac-like tegulum, seminal duct not meandering, embolus of variable length. Lateral tibial apophysis short. In *planissima* (Fig.2F-J), *grassalis* (Fig.2K-Q) and *panthera* (Fig.2R) groups dorsal tibial apophysis missing, but dorsolateral one present. *Holoplatys invenusta* with cymbial flange. Palpal organ of *complanata* group

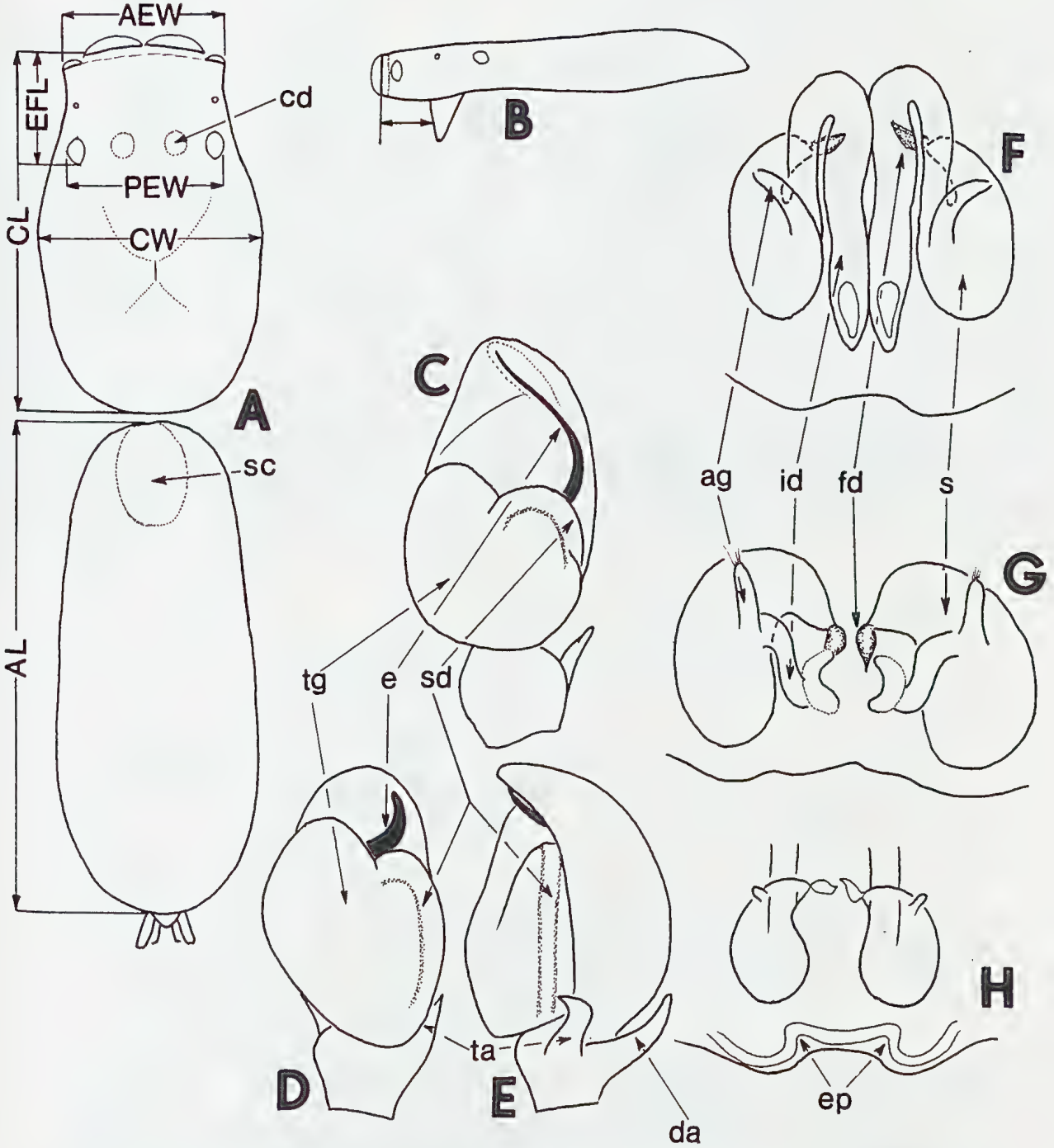



**Fig.1.** Morphological characters of *Holoplatys*: A – dorsal view, B – lateral view of cephalothorax, C-E – palpal organ, F-H – female genitalia. (Abbreviations in the text).

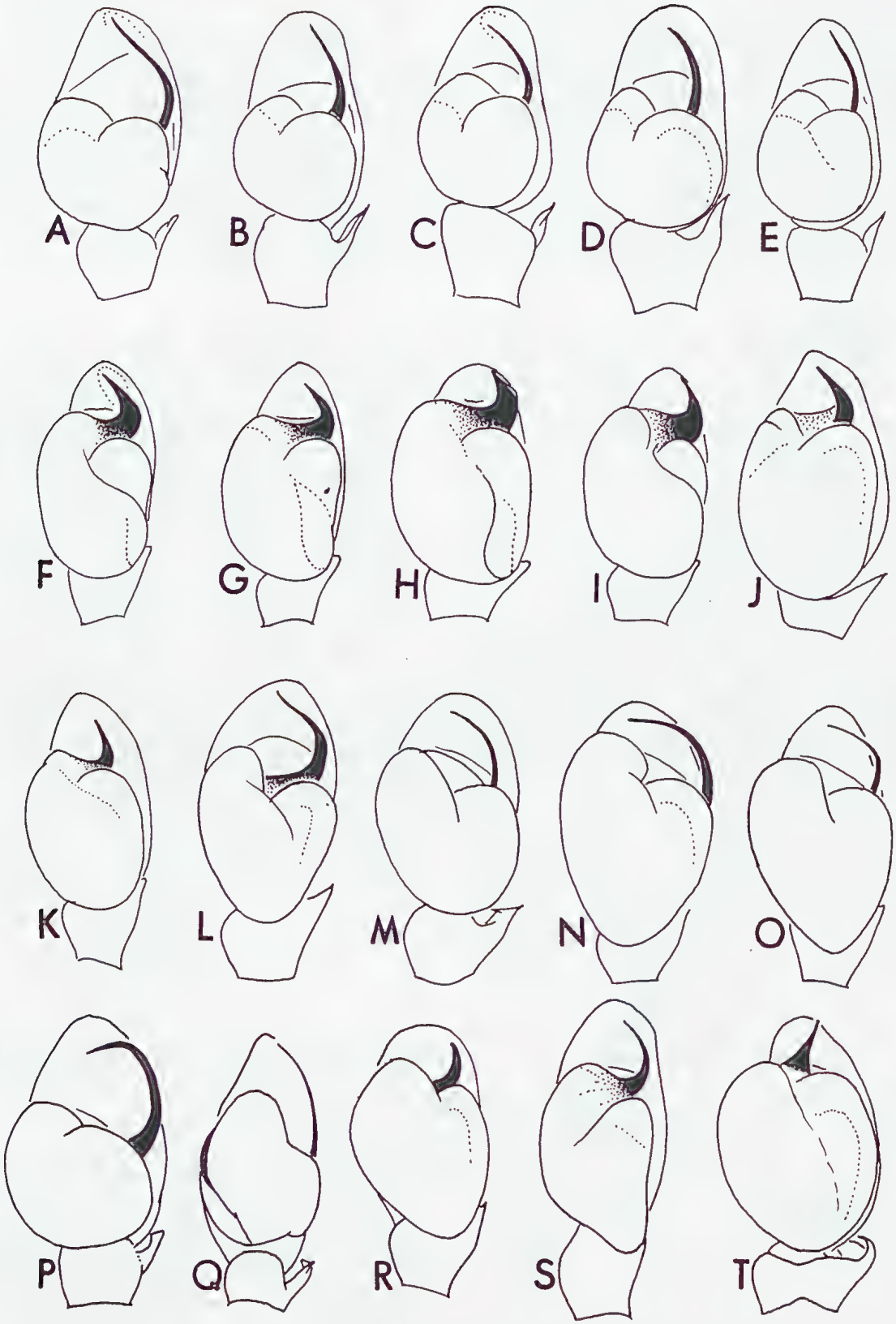



**Fig.2.** Morphological series of palpal organs in the genus *Holoplatys*. *complanata* group: A – *H. complanata*, B – *H. pedder*, C – *H. colemani*, D – *H. senilis*, E – *H. semiplanata*, *planissima* group: F – *H. mascordi*, G – *H. planissima*, H – *H. strzeleckii*, I – *H. pemberton*, J – *H. fusca*, *grassalis* group: K – *H. grassalis*, L – *H. chudalupensis*, M – *H. daviesae*, N – *H. dejongi*, O – *H. kalgoorlie*, P – *H. embolica*, Q – *H. lhotskyi*, *panthera* group: R – *H. queenslandica*, *bicolor* group: S – *H. bicolor*, *invenusta* group: T – *H. invenusta*.

(Fig.2A-E) similar to that in the genus *Ocrisiona* Simon. Epigyne and internal genitalia uniform in structure. Copulatory openings usually clearly visible, more or less distant from the epigastric furrow. Insemination ducts usually long. Spermathecae pear-shaped. Accessory glands relatively large, straight or curved, their shape and position of diagnostic value. Fertilisation ducts distinct. Posterior margin of epiqyne indented or not, sometimes accompanied by pockets.

## Biology and Relationships

To better understand the morphology, number of species and relationships of *Holoplatys*, the climatic, vegetational and topographic history of Australia have to be considered. As a result of the onset of dryer climatic conditions in the late Tertiary and Quaternary the range of loose-barked trees (mainly *Eucalyptus*) increased enormously, providing good conditions for explosive speciation of bark inhabitants. Hypothetically, the ancestors of *Holoplatys* were probably morphologically similar to other genera of jumping spiders but specialised as crevice dwellers became dorsally compressed to efficiently utilise narrow under-bark spaces. With the exception of bark dwellers, single species have been collected on herbs and grass. Jackson & Harding (1982) note that the rolled-up leaves of the New Zealand flax (*Phormium tenax*) are a habitat of two undescribed species. The same paper provides interesting behavioural studies - the only available for the genus.

*Ocrisiona* seems the closest relative of *Holoplatys* (Zabka, 1990). The genital structure of both genera is similar to that of species of the *complanata* group. Other species groups show reduced body size, tibial spines and cheliceral teeth and seem to be more specialised. Some other genera (including new ones) resemble *Holoplatys* in body form, and female genitalia, but their leg spination and palpal organs are usually different (Zabka, in preparation).

## Distribution

The distribution of *Holoplatys* (Maps 1-9) is restricted to Australia, adjacent areas and New Zealand. *Holoplatys complanata* (L. K.), *H. jardinensis* n.sp. and *H. queenslandica* n.sp. are Australian species occurring in Papua New Guinea (Port Moresby area), and *H. semiplanata* n.sp. has also been recorded from New Caledonia. *Holoplatys senilis* Dalmas has been described from New Zealand and at least two other species from the area require description (Jackson & Harding, 1982). In fact, insufficient knowledge of the salticid fauna of large parts of the region prevents useful comment on the zoogeographic history of the genus. The maps of distribution given are preliminary and tend to reflect main centres of arachnological activity rather then real distribution ranges. For some widely distributed species ranges may have changed during the period of human activity and settlement. Timber transports, for example, could have been an excellent artificial dispersal mechanism. Natural colonisation by ballooning is a possible explanation for large distributions in spiders but there is no evidence for this in *Holoplatys*. Strongly bark adapted animals seem rather unlikely candidates for ballooning dispersal anyway.

## Key to Species Groups of *Holoplatys*

1. Palpal organ without dorsal tibial apophysis ..... 2

—— Dorsal apophysis present ..... 3

2. Medium to large spiders (5.70-10.60), tegulum without lobe ..... 4

—— Smaller spiders, cephalothorax relatively high, tegulum elongate, with posterior lobe ..... *bicolor* group

3. Tiny to medium spiders (2.23-4.89), embolus delicate, in most species thin and long. If embolus different cephalothorax almost parallel-sided and its thoracic part up to 72% of total length ..... 5

—— Spiders larger (4.21-8.11), embolus massive, crescent-like, epigynal depression with distinctive margins ..... *planissima* group

4. Embolus long and thin, black spiders or with abdominal herring-bone pattern, sometimes tibial spines present, shallow epigynal depression with no distinctive margins ..... *complanata* group

—— Embolus shorter and tegulum larger than in the *complanata* group, dorsolateral tibial apophysis present, cymbium with flange, insemination ducts short and vast, spermathecae large ..... *invenusta* group

5. Embolus usually thin and long or very long, epigyne similiar to the *planissima* group ..... *grassalis* group

—— Embolus shorter, cephalothorax more elongate than in other groups, almost parallel-sided ..... *panthera* group

## The *complanata* Group

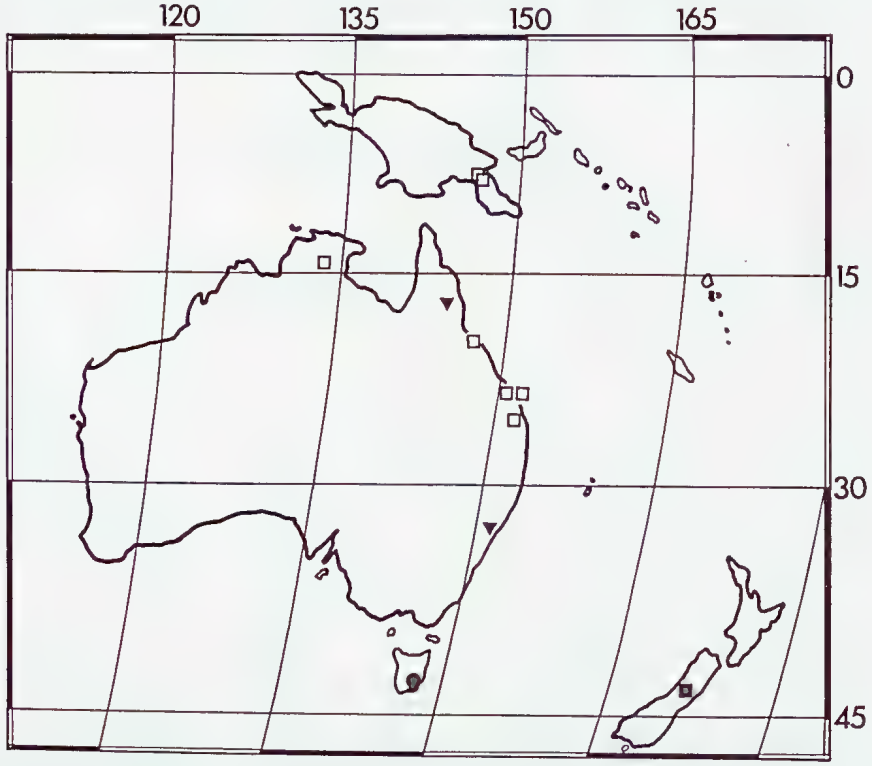
The group consists of 14 species, widespread from north Queensland through New South Wales to Western Australia. Single specimens of two species have also been recorded from Papua New Guinea, New Caledonia and New Zealand.

With the exception of *H. senilis* Dalmas, *H. pedder* n.sp. and *H. colemani* n.sp., all species show an abdominal mosaic with central dark stripe and herring-bone pattern. Body size 5.50-10.60 mm. Palpal organ without dorsal tibial apophysis, embolus long and thin. Epigynal depression with no distinctive margins. Insemination ducts long or very long. Tibial spines on legs I and (or) II usually absent but present in *H. pedder* n.sp., *H. senilis* Dalmas and *H. windjanensis* n.sp. General pattern of genitalic structure almost identical to that found in the genus *Ocrisiona*. Species included: *complanata, pedder, senilis, colemani, complanatiformis, canberra, jardinensis, bramptonensis, rainbowi, meda, semiplanata, oakensis, kempensis, windjanensis.*

### ***Holoplatys complanata*** (L. Koch) n.comb.

Figs 3-6, Map 1

*Marptusa complanata* L. Koch, 1879: 1093.
*Ocrisiona complanata*.–Simon, 1901: 602.




Map 1. Inverted closed triangle – *H. colemani* n.sp.; open square – *H. complanata* (L. Koch); closed circle – *H. pedder* n.sp.; closed square – *H. senilis* (Dalmas).

**Material examined.** Queensland: SYNTYPES, 2 males, female, Port Mackay, Rockhampton, Gayndah, (Mus. Godeffroy 16522), ZMH; female, Tryon Island, 21 Aug. 1977, M. Jahnke, QMB S3582; female, Tryon Island, 21-29 Aug. 1971, H. Heatwole, QMB S3633; male, Homevale, beating vine thicket, 1-7 Apr. 1975, V. Davies, QMB S4611. Northern Territory: female, Roper River, M.J. Colclough, QMB W2137(a). Papua New Guinea: male, Izzy Dizzy Creek, Morobe Province, under bark of *Araucaria cunninghami*, 24 Sept. 1970, B. Gray, AMS KS18860; female, Bulolo, Morobe Province, 18 Aug. 1970, B. Gray, AMS KS 13220.

**Diagnosis.** Unlike *pedder, senilis* and *colemani* - herring-bone abdominal pattern present and embolus longer than *semiplanata.* Accessory glands laterally curved and join the spermathecae on their inner walls.

**Male** (Fig.3A). Eye field black, thorax dark-brown,

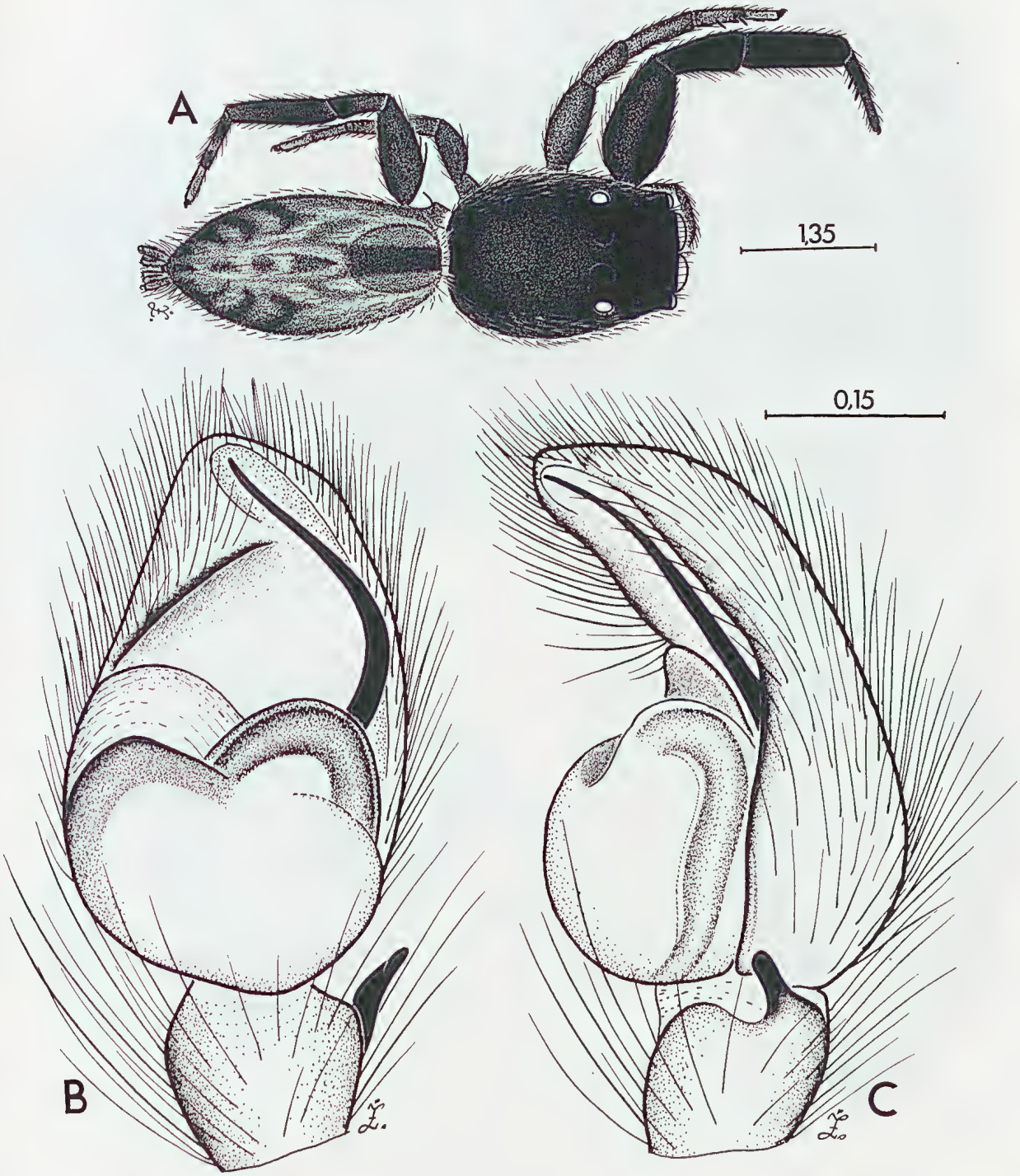



**Fig.3.** *Holoplatys complanata*, male (syntype).

numerous white hairs along lateral surfaces. Abdomen with orange anterior scutum and dark-grey pattern on yellowish or beige background. Spinnerets grey. Clypeus dark-brown with whitish hairs. Chelicerae dark-brown with transverse stripe of white setae proximally. Maxillae and labium dark-brown, the last with light tips. Sternum dark-brown, venter dark-grey. Legs I black-brown, others slightly lighter, especially their distal segments.

Palpal organ (Fig.3B,C) with long embolus, tegulum

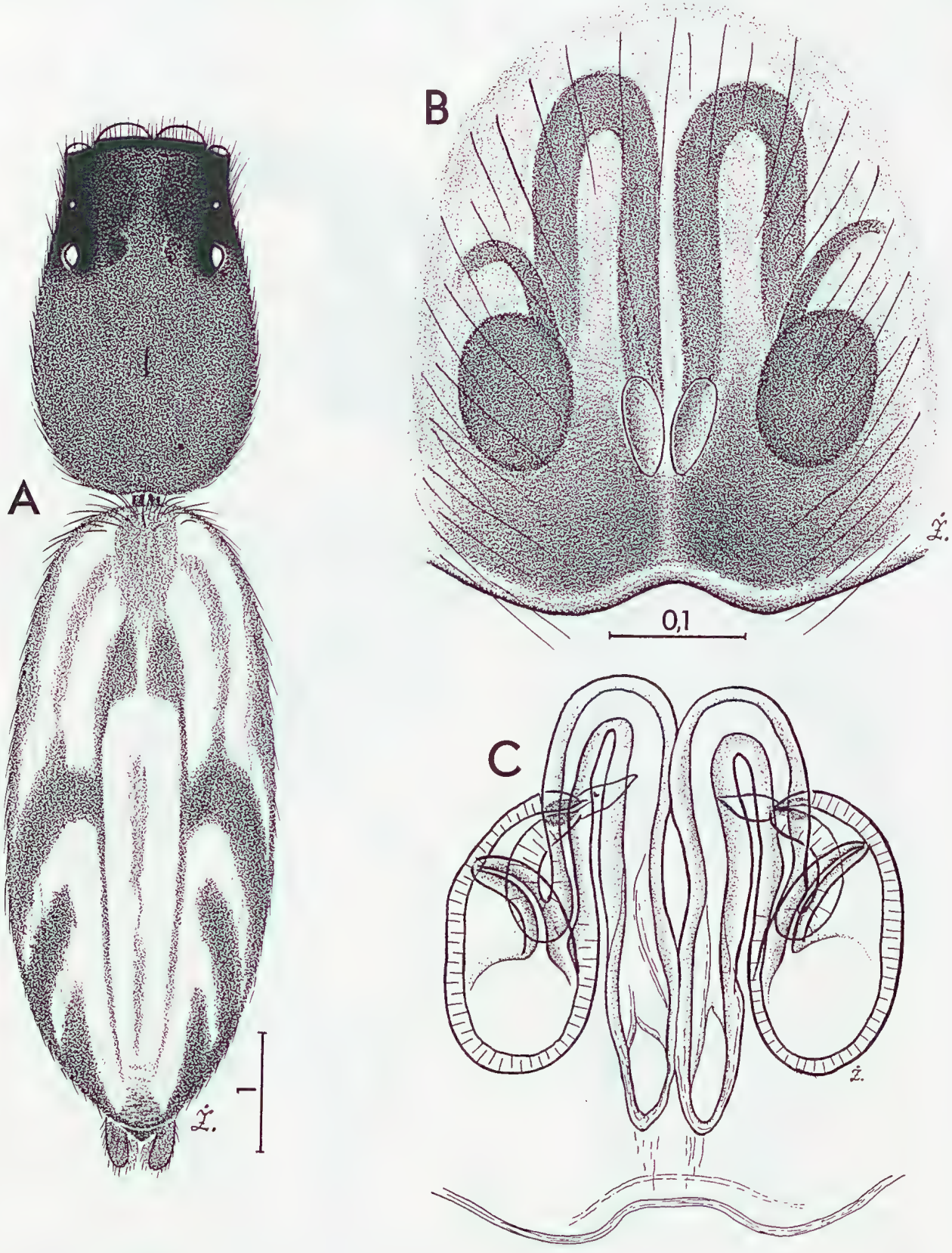



**Fig.4.** *Holoplatys complanata*, female (syntype).

oval and wide.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r0-0 or r1-1.

*Dimensions.* CL 2.24-2.90 (2.48), CW 1.46-1.84 (1.60), CW/CL 0.63-0.67 (0.64), EFL 0.73-0.92 (0.81), EFL/CL 0.31-0.35 (0.32), AEW 1.15-1.38 (1.22), PEW 1.18-1.38 (1.25), AL 2.83-3.60 (3.42).

**Female** (Figs 4A, 5A, 6A). Cephalothorax brown with darker surrounding of eyes. Abdomen with beige and grey-brown pattern. Clypeus, chelicerae and maxillae brown, the last with yellow tips. Labium brown, sternum

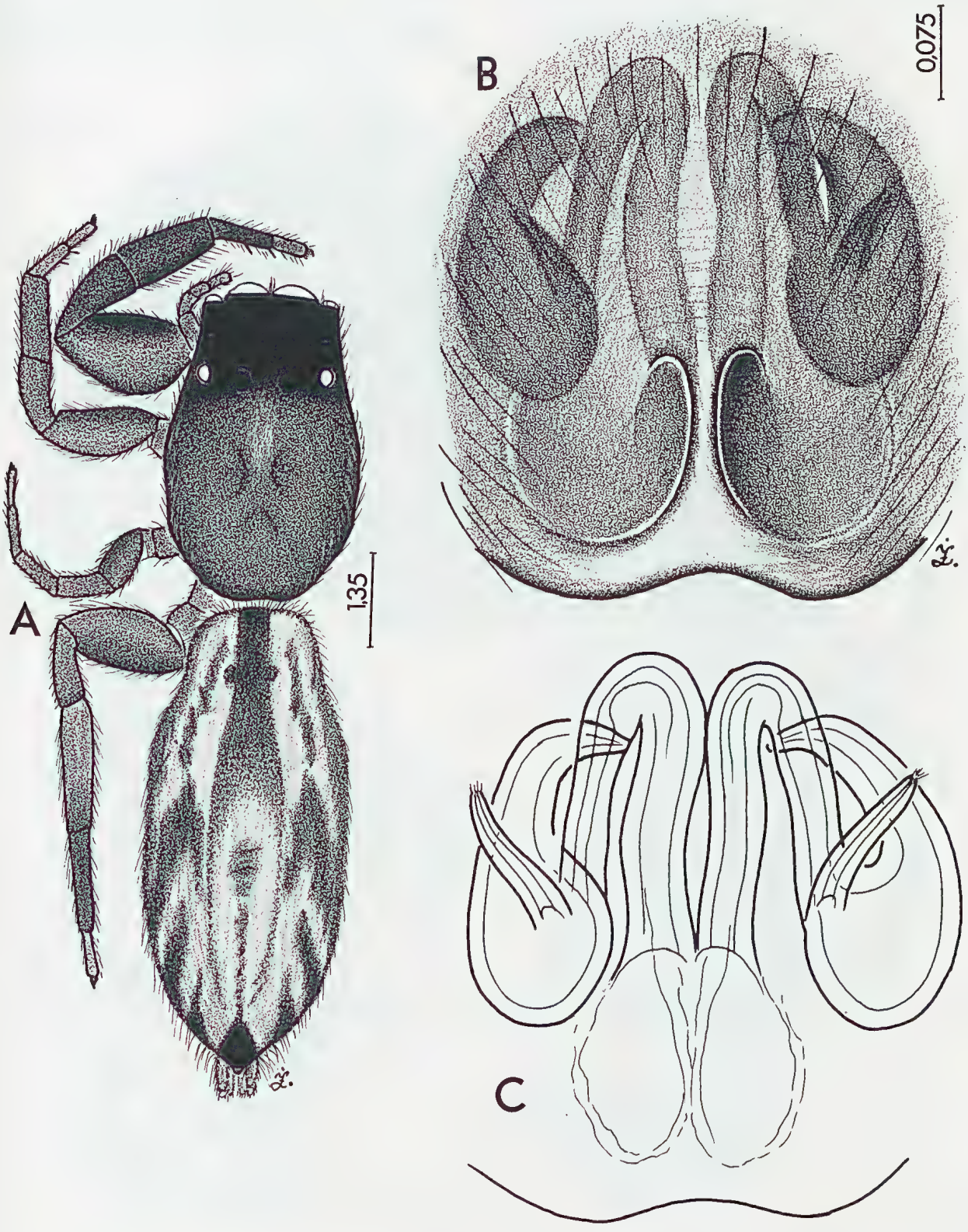



**Fig.5.** *Holoplatys complanata*, female from Bulolo.

light-brown, venter beige. Legs brown, dorsoventrally darker, distally lighter.

Genitalia (Figs 4B,C, 5B,C, 6B,C) with long insemination ducts, accessory glands curved laterally, located on inner walls of spermathecae.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r1-1.

*Dimensions.* CL 3.03-4.36 (3.87), CW 1.88-2.80 (2.44), CW/CL 0.62-0.64 (0.62), EFL 0.99-1.32 (1.19), EFL/CL 0.29-0.32 (0.31), AEW 1.38-1.84 (1.67), PEW 1.41-1.91 (1.72), AL 5.41-6.40 (5.90).

### *Holoplatys pedder* n.sp.

Fig.7, Map 1

**Material examined.** Tasmania: HOLOTYPE, male, Lake Pedder, II.1967, A.J. Dartnall, TMH J.588.

**Diagnosis.** Black, slender spider. White hairs along cephalothorax form medial and marginal stripes. No

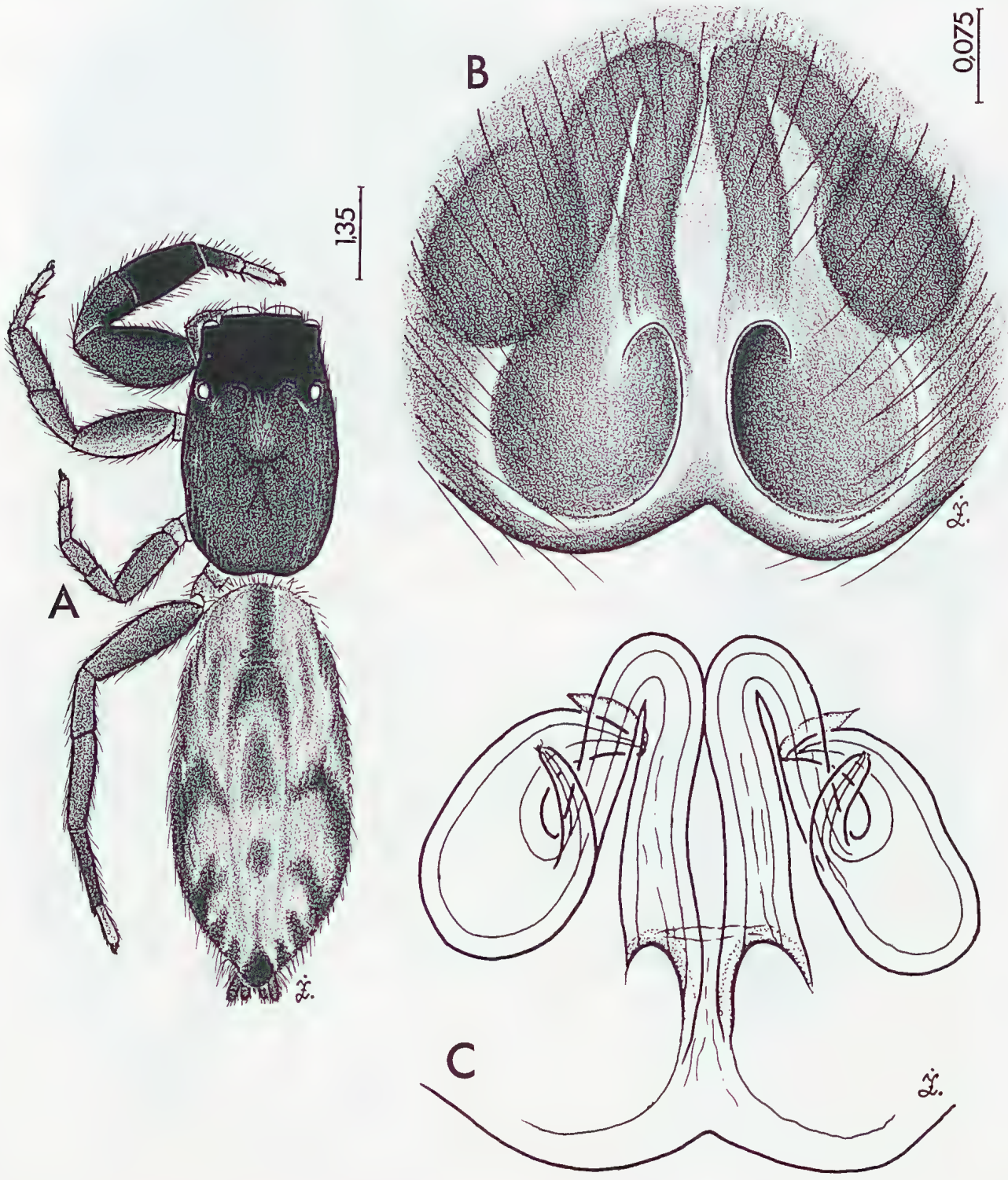



**Fig.6.** *Holoplatys complanata*, female from Tryon Island.

distinct scutum on abdomen, tibia I with single prolateral spine.

**Male** (Fig.7A). Cephalothorax black with central and marginal stripes of white hairs, its anterior part more sclerotised but without distinct scutum. Spinnerets black. Clypeus brown with white hairs centrally. Chelicerae brown, maxillae, labium and sternum dirty-brown. Venter grey-brown. Legs brown, lighter distally, lateral surfaces darker, white and brown hairs numerous.

Palpal organ (Fig.7B,C) almost identical to *senilis* and *colemani*.

*Leg spination.* tI: p0-1; mI: p1-1, r1-1; mII:, p1-1, r0-1.

*Dimensions.* CL 3.12, CW 0.91, CW/CL 0.61, EFL 0.96, EFL/CL 0.30, AEW 1.32, PEW 1.34, AL 3.70.

**Female.** The female is unknown.

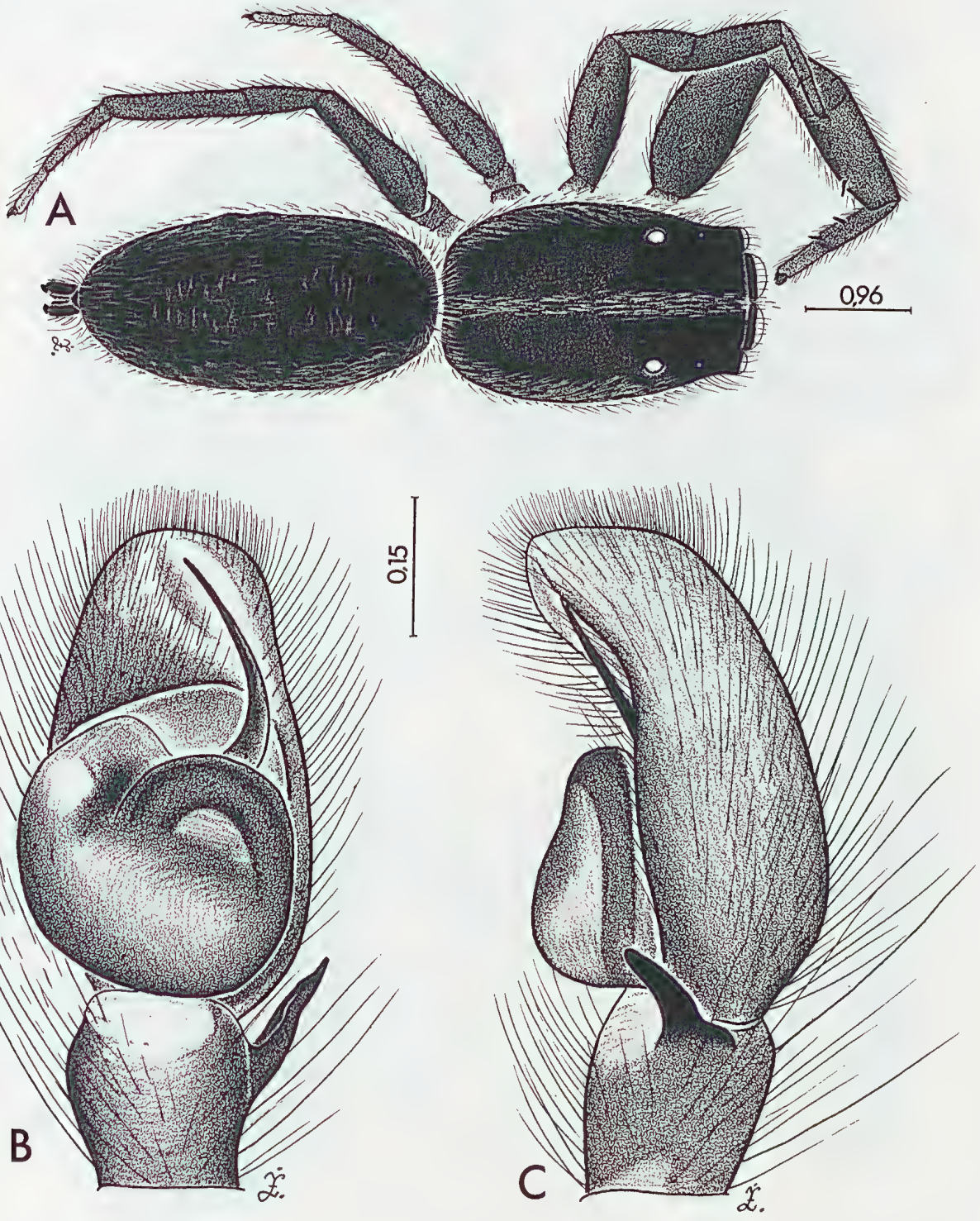



**Fig.7.** *Holoplatys pedder*, male (holotype).

***Holoplatys senilis*** Dalmas

Figs 8,9, Map 1

*Holoplatys senilis* Dalmas, 1917: 416.

**Material examined.** New Zealand: male, female, MNHN B2341. Probably type-material but neither specimen's status nor locality marked on the original label.

**Diagnosis.** In comparison to *pedder* median stripe on

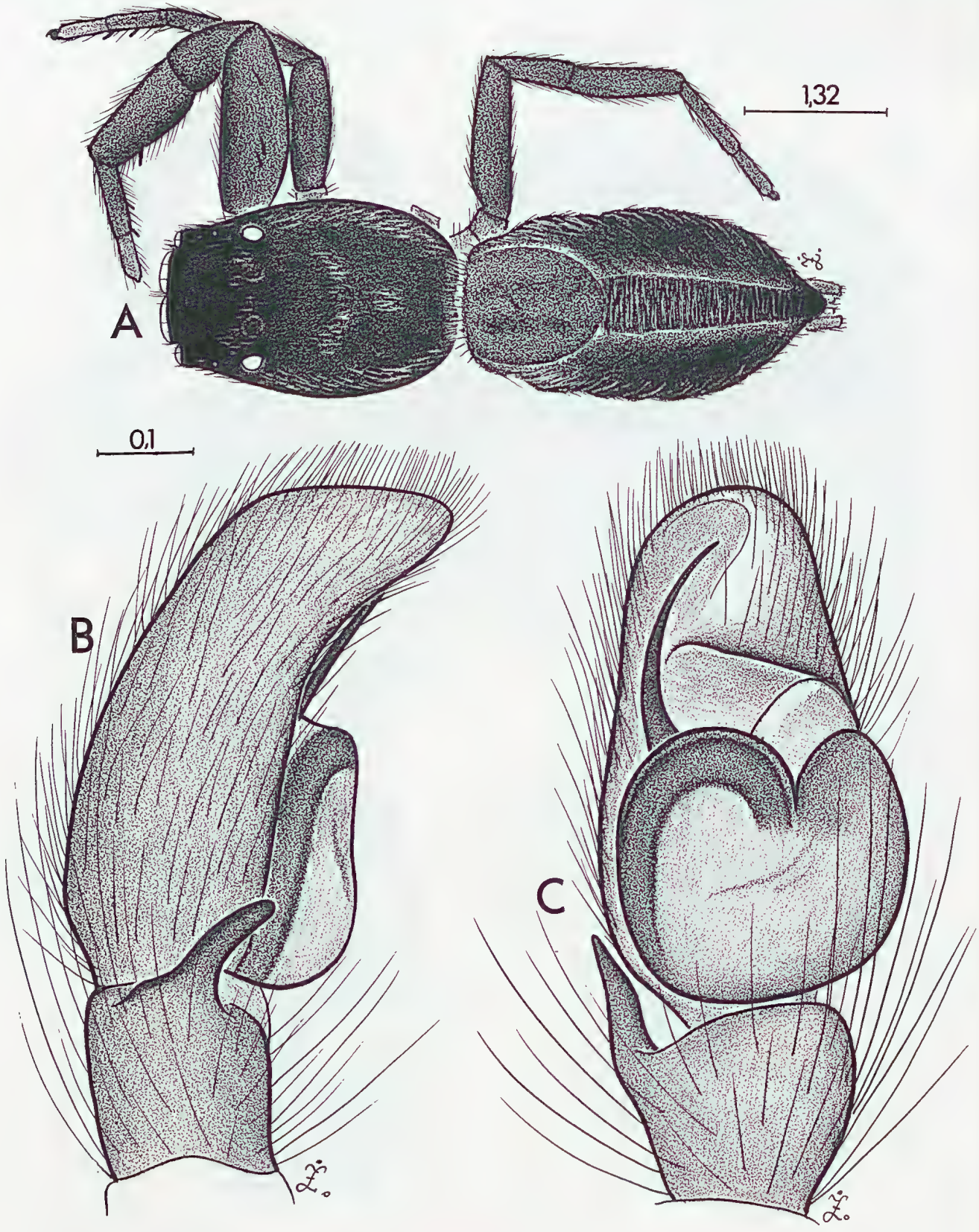



**Fig.8.** *Holoplatys senilis*, male (type?) from New Zealand.

cephalothorax less distinct, anterior abdominal scutum better marked. Tibia I with a single prolateral spine. Insemination ducts relatively short.

**Male** (Fig.8A). Eye field black, thorax dark-brown with scattered white hairs more numerous marginally. Abdomen generally dirty-brown with large anterior scutum and lighter posterior lines. Spinnerets grey-brown. Clypeus dark-brown with cluster of white hairs centrally. Chelicerae dark-brown with transverse stripe of white hairs in their basal parts. Maxillae brown with lighter tips, labium dark-brown, sternum brown, venter grey. Legs I dark-brown, distally gradually lighter. Other legs slightly lighter.

Palpal organ (Fig.8B,C) similiar to *pedder*.

*Leg spination.* tI: p0-1; mI: p1-1, r1-1; mII; p1-1, r1-1.

*Dimensions.* CL 2.70, CW 1.81, CW/CL 0.67, EFL 0.85, EFL/CL 0.31, AEW 1.28, PEW 1.28, AL 3.36.

**Female** (Fig.9C). Cephalothorax coloured as in male with white hairs scattered on eye field and more numerous in fovea region and marginally. Abdomen dark, grey-brown with whitish and brown hairs. Spinnerets

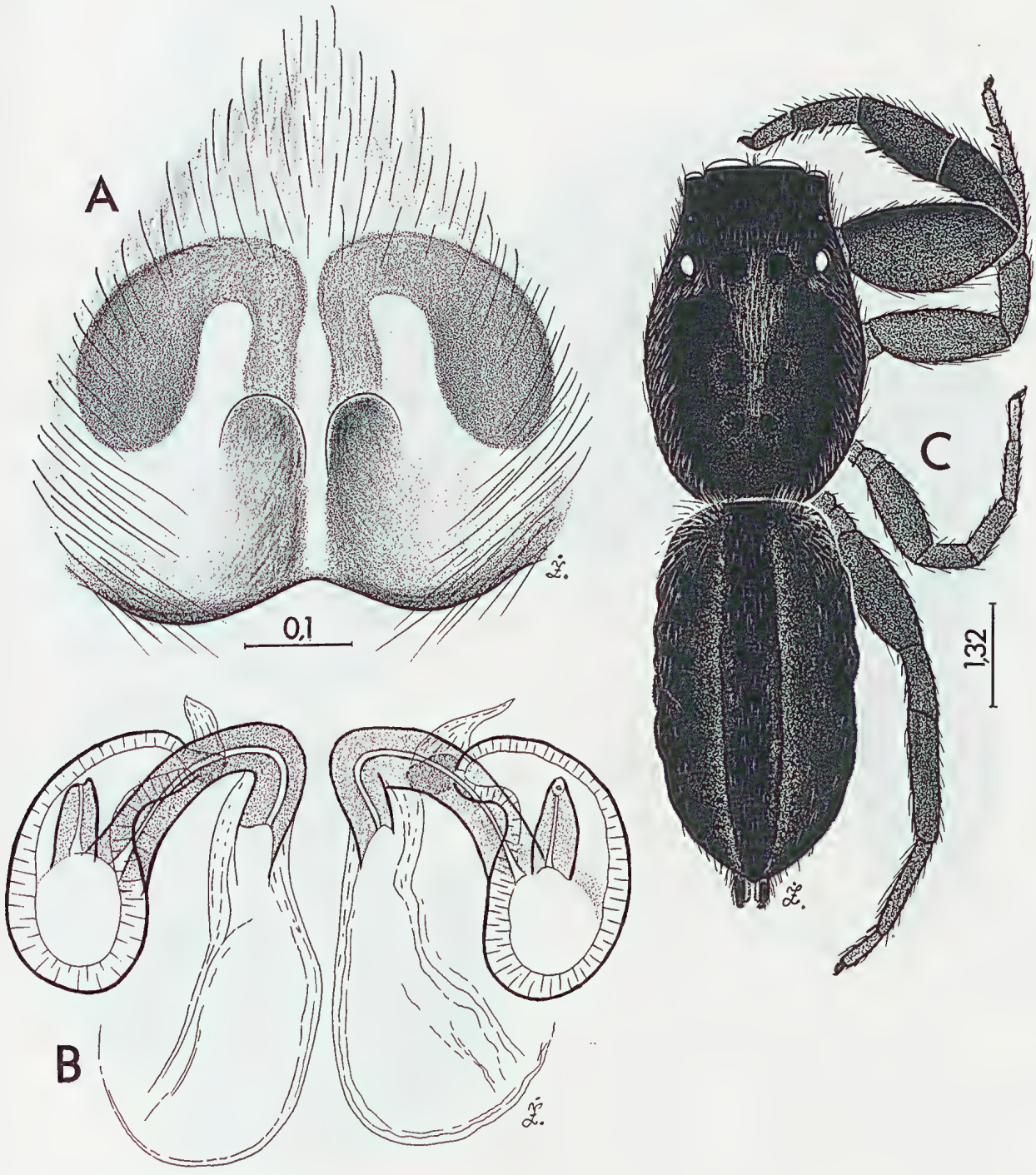



**Fig.9.** *Holoplatys senilis*, female (type?) from New Zealand.

black-brown. Clypeus and chelicerae black-brown, the first with light scattered hairs. Pedipalps dark-orange with white and yellow hairs. Maxillae and labium black-brown, lighter distally with yellow tips, sternum black-brown, venter grey-black. Legs I dark-brown, lighter distally, hairs rather numerous, light and brown.

Genitalia (Fig.9A-B) with insemination ducts shorter than in other species, accessory glands straight.

*Leg spination.* tI: p0-1, r0-0; mI p1-1, r1-1; mII: p1-1, r1-1.

*Dimensions.* CL 4.35, CW 2.83, CW/CL 0.65, EFL 1.25, EFL/CL 0.29, AEW 1.74, PEW 1.91, AL 4.68.

### *Holoplatys colemani* n.sp.

Figs 10,11, Map 1

**Material examined.** Queensland: HOLOTYPE, male,

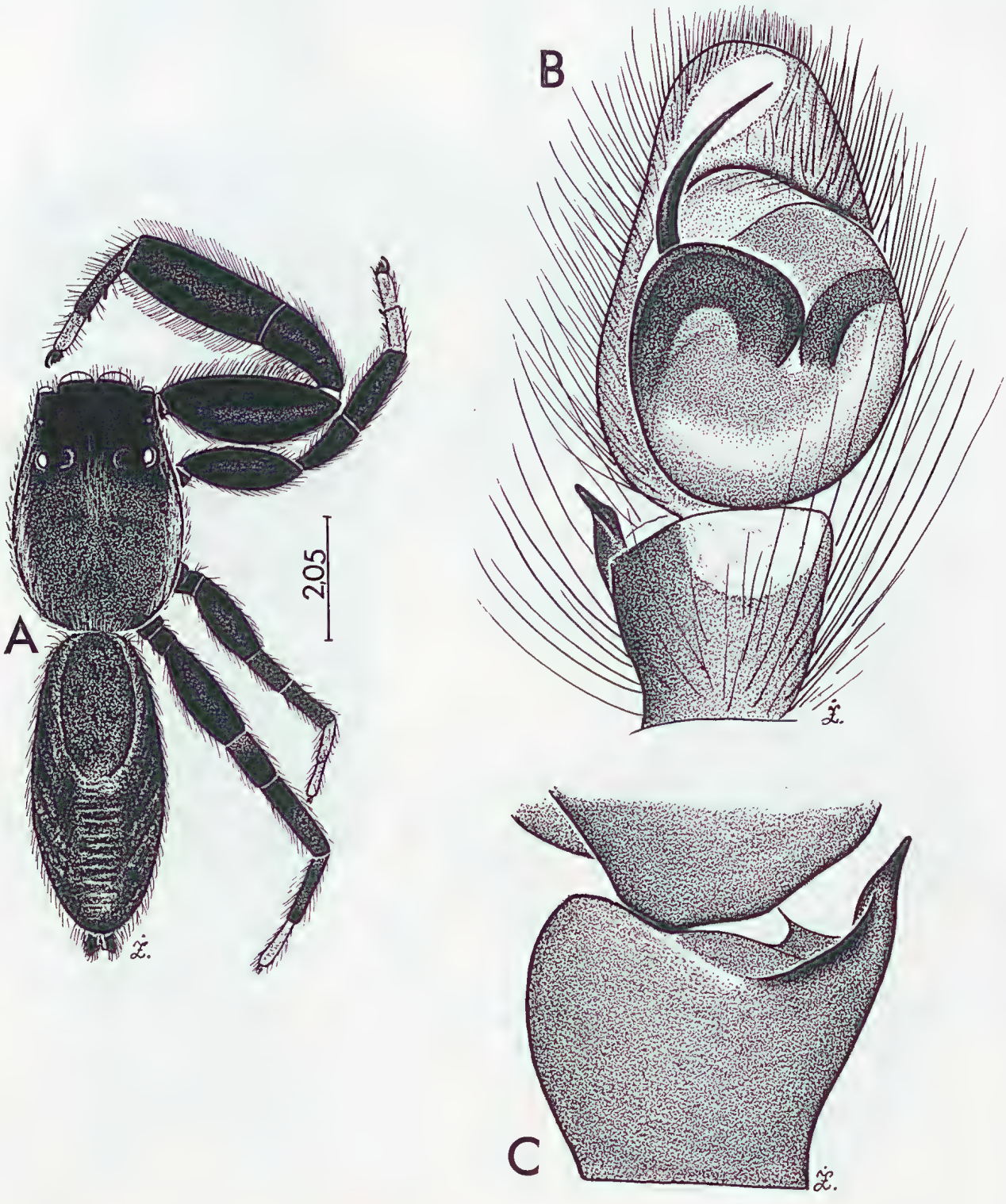



**Fig.10.** *Holoplatys colemani*, male (holotype).

ALLOTYPE, female, Wolfram, 3 May 1977, N.C. Coleman, AMS KS18815, KS19119. New South Wales: PARATYPES, male, Botany, 10 Dec. 1978, R. Mascord, AMS KS4140.

**Etymology.** The specific name is proposed in honour of N. Clyde Coleman, Australian naturalist, collector of the part of the material studied.

**Diagnosis.** Dark spider but without median stripe on cephalothorax. In male first legs fringed, abdominal scutum present. Spines on tibia I missing.

**Male** (Fig.10A). Dark-brown spider with white hairs around margins of cephalothorax. Abdomen with large anterior scutum. Clypeus black-brown with long light and dark hairs. Chelicerae dark-brown with transverse stripe of white hairs. Maxillae and labium dark-brown with yellow tips, sternum brown, venter greyish-black. Legs I fringed, black-brown, distal parts of tarsi orange. Other legs lighter.

Palpal organ as in Figure 10B,C.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r1-1 or 0-0 or 0-1.

*Dimensions.* CL 3.23-4.15 (3.69), CW 2.11-2.84 (2.47), CW/CL 0.65-0.68 (0.67), EFL 1.00-1.18 (1.09), EFL/CL 0.28-0.30 (0.29), AEW 1.48-1.85 (1.66), PEW

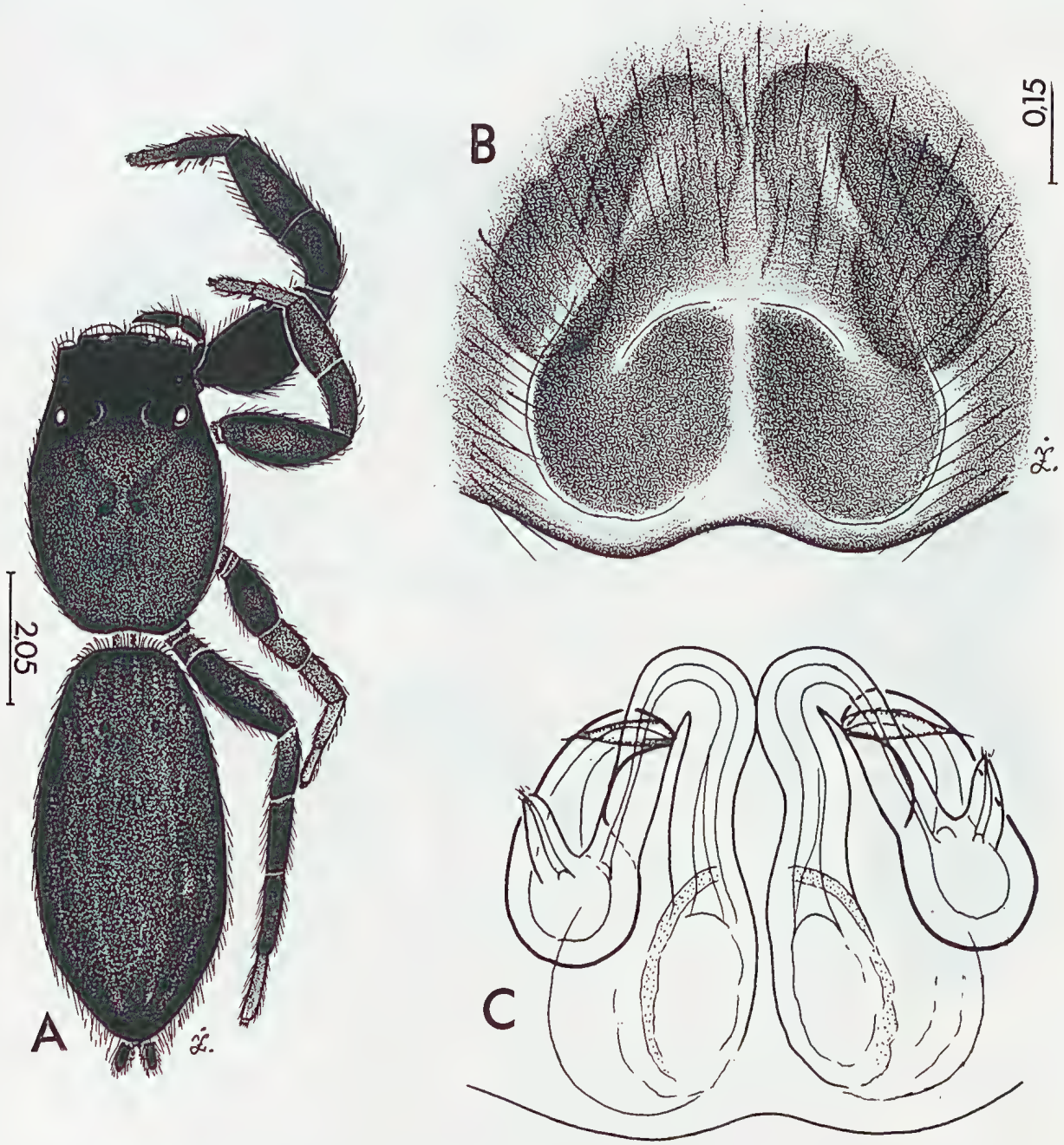



**Fig.11.** *Holoplatys colemani*, female (allotype).

1.51-1.91 (1.71), AL 3.76-5.08 (4.42).

**Female** (Fig.11A) generally as male but white marginal hairs less numerous and abdominal scutum absent. Clypeus brown-black with long hairs of the same colour. Chelicerae, maxillae, labium and sternum dark-brown, the first without frontal white hairs. Venter grey, with 2 longitudinal rows of lighter spots. Legs coloured as in male but shorter, legs I not fringed.

Genitalia (Fig.11B,C) very similar to other species of the group, especially to *semiplanata*.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 4.55, CW 2.97, CL/CW 0.65, EFL 1.25, EFL/CL 0.27, AEW 1.98, PEW 2.04, AL 6.07.

### *Holoplatys complanatiformis* n.sp.

Fig.12, Map 2

**Material examined.** Queensland: HOLOTYPE, female, Lake Broadwater, Surveyors Gully, under bark, 27 Jan. 1985, M. Bennie, V. Davies, QMB S6760; PARATYPES, female, Brisbane, wasp nest, 24 Apr. 1974, V. Davies, QMB S4603. New South Wales: PARATYPES, female, Dubbo, 31 July 1966, AMS KS19120.

**Diagnosis.** Abdominal pattern present but darker than in related species. In comparison to *complanata* insemination ducts shorter, join the spermathecae on their lateral walls and position of accessory glands different.

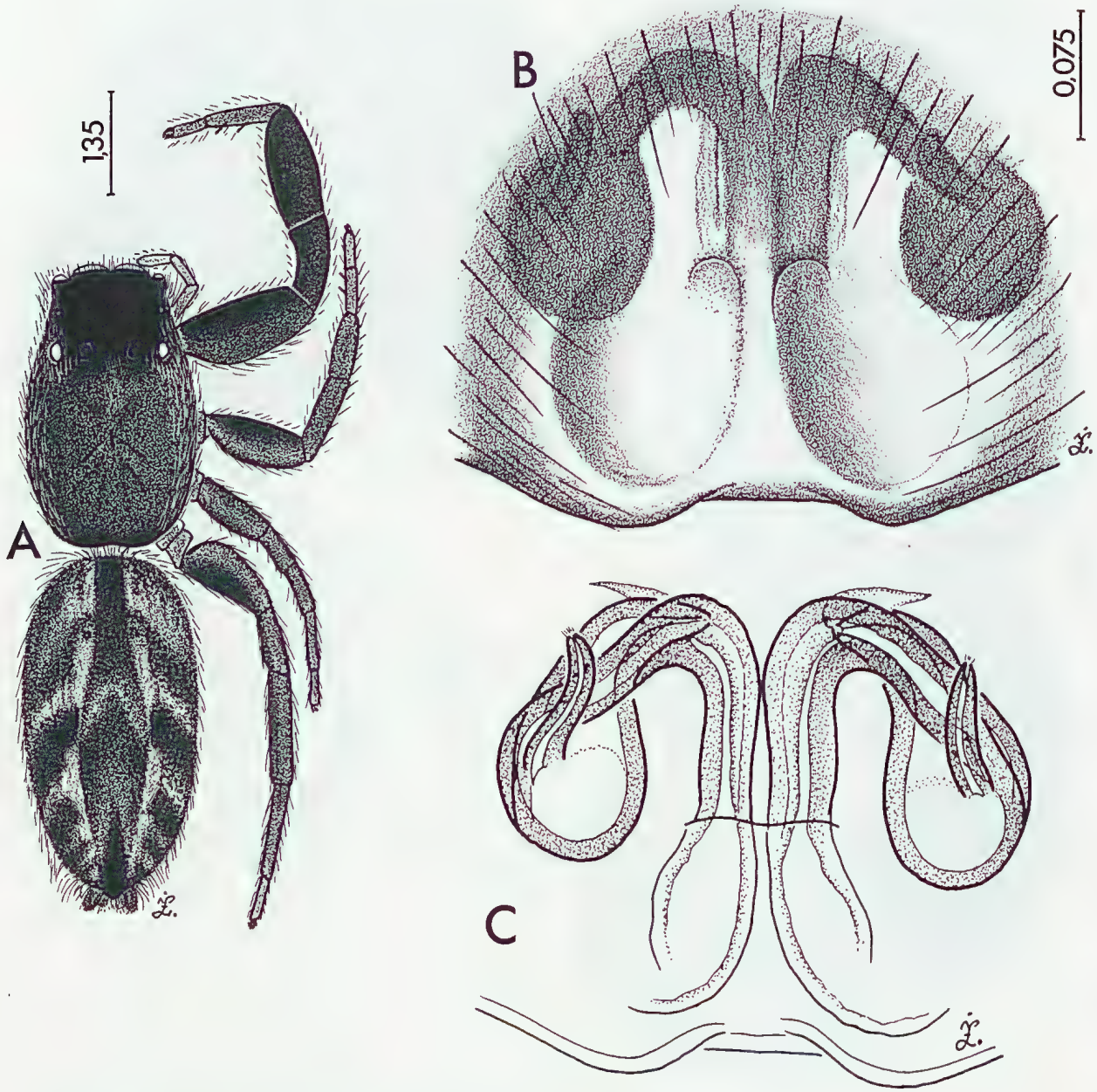



**Fig.12.** *Holoplatys complanatiformis*, dorsal body of female (holotype) and genitalia of paratype from Brisbane.

**Male.** The male is unknown.

**Female** (Fig.12A). Eye field dark-brown, thorax brown. Numerous white hairs on lateral surfaces of cephalothorax. Abdomen with light and dark-grey pattern, covered with numerous grey-brown and white hairs. Spinnerets greyish. Clypeus dark-brown with long white hairs, without fringe. Chelicerae, maxillae, labium and sternum dirty-brown, venter beige. Pedipalps yellow, darker distally with white hairs. Legs I dark-brown, lighter distally, darker laterally, other legs similar in colour.

Genitalia as in Figure 12B,C. In comparison to related species insemination ducts and accessory glands different.

*Leg spination.* mI: p1-1, r1-1; mII p1-1, r1-1.

*Dimensions.* CL 3.23-3.63 (3.43), CW 2.08-2.37 (2.22), CW/CL 0.64-0.70 (0.67), EFL 1.00-1.12 (1.06), EFL/CL 0.30-0.31 (0.31), AEW 1.42-1.51 (1.46), PEW 1.59-1.65 (1.62), AL 4.29-4.35 (4.32).

### *Holoplatys canberra* n.sp.

Fig.13, Map 2

**Material examined.** Australian Capital Territory: HOLOTYPE, female, Canberra, Dec. 1980, home wall, E. McCallan, QMB S4609.

**Diagnosis.** Closely related to *complanatiformis* but abdomen lighter and accessory glands much longer.

**Male.** The male is unknown.

**Female** (Fig.13A). Eye field dark-brown, thorax lighter. Around fovea and marginally white hairs present. Abdomen lighter than in *complanatiformis*. Spinnerets grey. Clypeus blackish with single long whitish hairs. Chelicerae brown, pedipalps orange with long white hairs. Maxillae brown with lighter tips, labium and sternum brown with darker margins. Venter light-grey with 2 longitudinal darker lines. Dorsal and ventral femora I and metatarsi orange, tarsi yellow, the rest dark-brown. Other legs lighter.

Genitalia (Fig.13B,C) with very long accessory glands, also distal part of spermathecae more elongate than in other species.

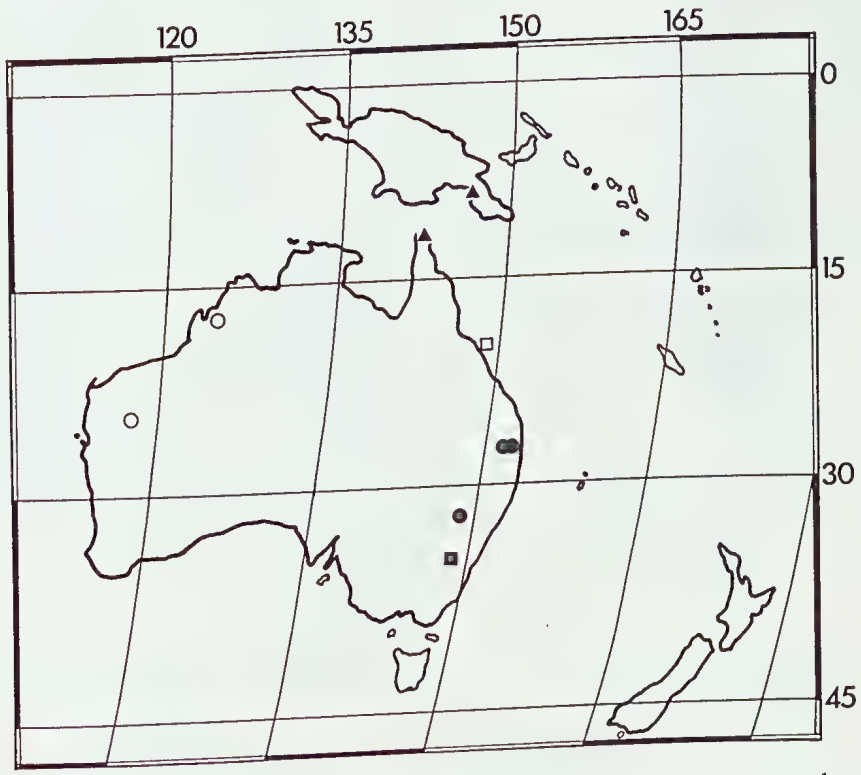
*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r1-1.

*Dimensions.* CL 2.88, CW 1.91, CW/CL 0.66, EFL 0.92, EFL/CL 0.32, AEW 1.26, PEW 1.38, AL 3.96.

### *Holoplatys jardinensis* n.sp.

Fig.14, Map 2

**Material examined.** Papua New Guinea: HOLOTYPE, female, Central Province, Waigani, Botanic Garden, under *Eucalyptus* bark, 28 June 1988, D. Court, M. Zabka, AMS KS 19016; PARATYPES, 5 females, juvenile, same data, AMS KS19017. Queensland: PARATYPE, female, Cape York, Jardine River, 26 Aug. 1985, M. Bennie, QMB S4564.




Map 2. Open square – *H. bramptonensis* n.sp.; closed square – *H. canberra* n.sp.; closed circle – *H. complanatiformis* n.sp.; closed triangle – *H. jardinensis* n.sp.; open circle – *H. meda* n.sp.

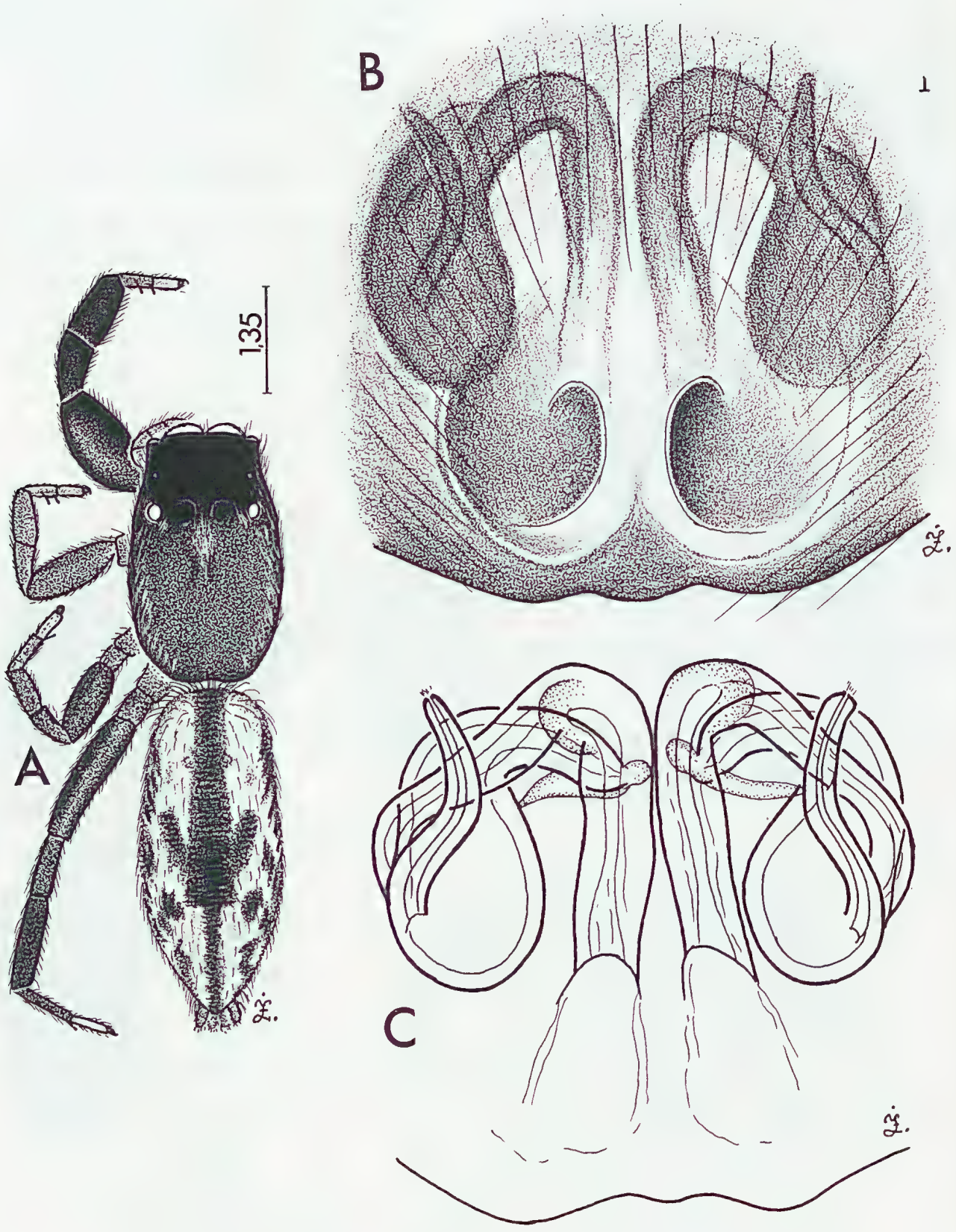



**Fig.13.** *Holoplatys canberra*, female (holotype).

**Diagnosis.** Insemination ducts twisted as in *bramptonensis* but distal parts of spermathecae different in shape. Accessory glands curved as in *complanata*.

**Male.** The male is unknown.

**Female** (Fig.14A). Eye field black, thorax brown, all covered with white hairs – more numerous laterally. Abdominal mosaic rather dark, spinnerets grey. Clypeus black, chelicerae dark-brown, maxillae, labium and sternum brown, venter beige. Legs I brown, others dirty-orange. All legs darker laterally and around joints.

Genitalia (Fig.14B,C) with long and twisted insemination ducts, fertilisation part of spermathecae narrow, accessory glands curved, located on inner walls of spermathecae.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r0-0 or 0-1 or 1-1.

*Dimensions.* CL 2.83-3.76 (3.21), CW 1.71-2.38 (1.99), CW/CL 0.60-0.63 (0.61), EFL 0.99-1.12 (1.02), EFL/CL 0.30-0.35 (0.32), AEW 1.32-1.65 (1.47), PEW 1.38-1.71 (1.53), AL 3.69-5.08 (4.53).

### *Holoplatys bramptonensis* n.sp.

Fig.15, Map 2

**Material examined.** Queensland: HOLOTYPE, female, Brampton Island, open *Eucalyptus* forest, 26 Feb. 1975, D.A. Schultz, QMB S3548.

**Diagnosis.** Insemination ducts twisted as in *jardinensis*

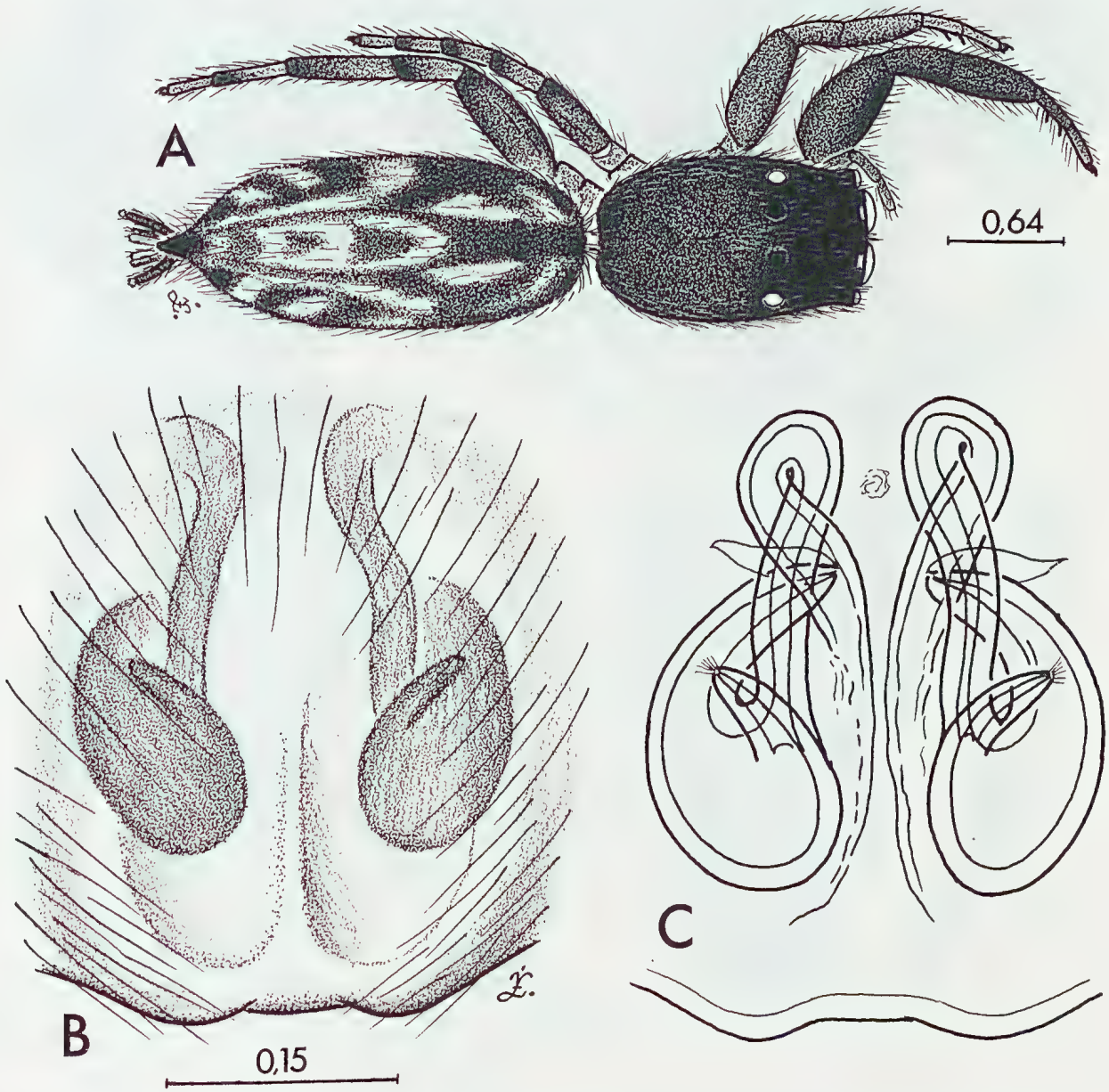



**Fig.14.** *Holoplatys jardinensis*, dorsal body of female (holotype) and genitalia of paratype from Jardine River.

but distal parts of spermathecae wider, also position and shape of accessory glands different.

**Male.** The male is unknown.

**Female** (Fig.15A). Eye field black-brown. Thorax brown, around fovea lighter, with cluster of white hairs, similar hairs also on lateral thorax. Abdomen with grey pattern on yellowish background. Spinnerets grey. Clypeus and chelicerae dark-brown, maxillae of the same colour with yellow tips, labium and sternum dirty-brown. Venter grey with 4 longitudinal rows of lighter spots. Legs I generally brown, darker on distal femur, patella, tibia and proximal metatarsus. Other legs lighter.

Genitalia (Fig.15B,C) with twisted insemination ducts, spermathecae vast, accessory glands rather short.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 3.30, CW 2.04, CW/CL 0.62, EFL

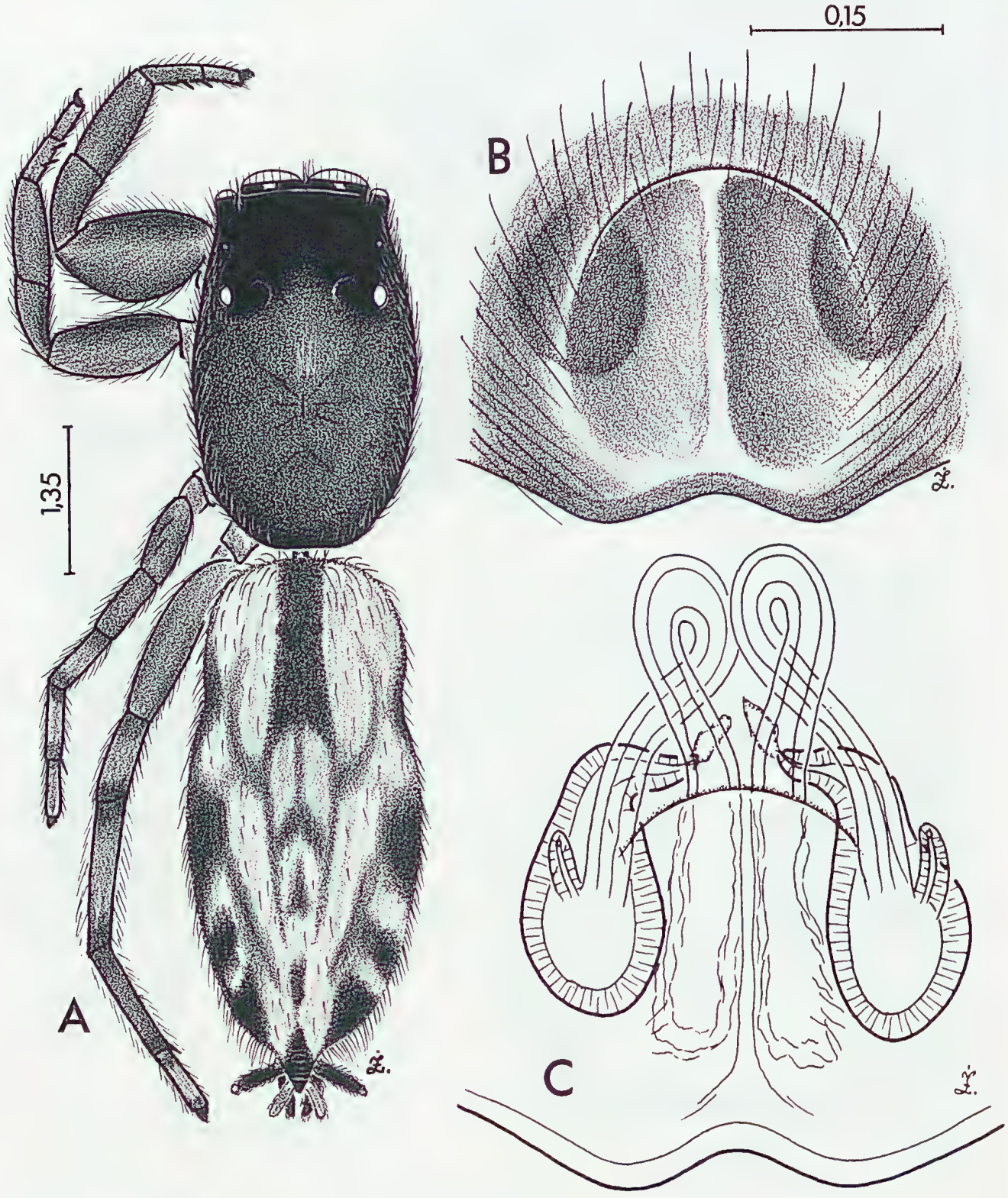



**Fig.15.** *Holoplatys bramptonensis*, female (holotype).

0.99, EFL/CL 0.30, AEW 1.55, PEW 1.58, AL 4.81.

### *Holoplatys rainbowi* n.sp.

Fig.16, Map 3

**Material examined.** Queensland: HOLOTYPE, female, Brisbane, Lake Broadwater, 26 Jan. 1985, M. Bennie, V. Davies, QMB S3594.

**Etymology.** The specific name is proposed in honour of William James Rainbow, former Entomologist at the Australian Museum, Sydney.

**Diagnosis.** Insemination ducts very long, spermathecae more elongated than in other species, accessory glands straight.

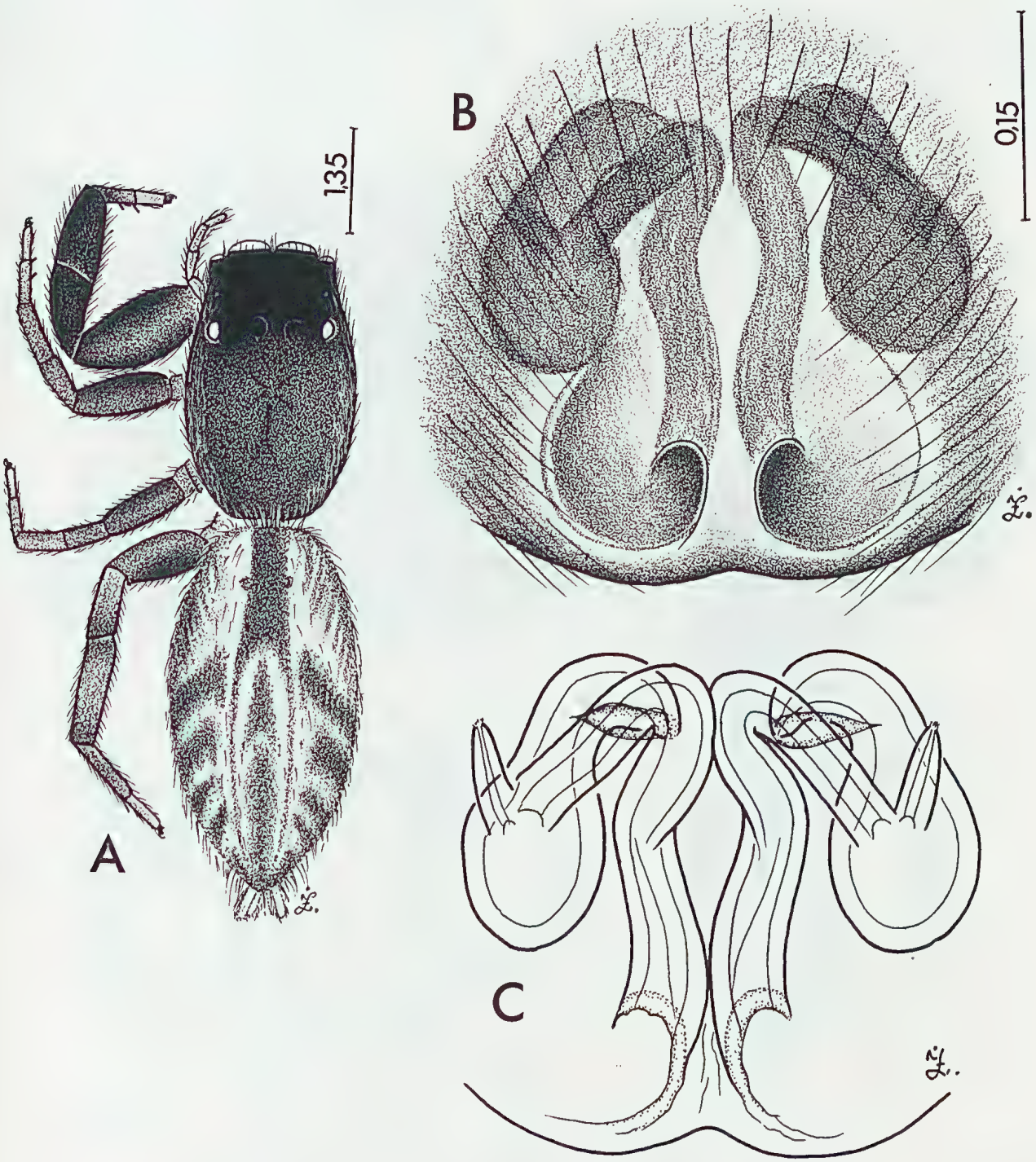



**Fig.16.** *Holoplatys rainbowi*, female (holotype).

**Male.** The male is unknown.

**Female** (Fig.16A). Eye field black-brown, thorax brown with white hairs on lateral surfaces. Abdomen with dark and yellowish-grey pattern. Spinnerets yellow-grey. Clypeus and chelicerae black-brown, maxillae and labium of the same colour with yellow tips, sternum dirty-brown, venter light-grey. Legs I generally brown, with darker distal part of femur, patella, tibia, proximal metatarsus. Other legs generally lighter, darker laterally and around joints.

Genitalia (Fig.16B,C) similar to *complanata, meda* and *semiplanata* but insemination ducts and spermathecae longer.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 3.36, CW 2.14, CW/CL 0.63, EFL 1.05, EFL/CL 0.31, AEW 1.51, PEW 1.58, AL 4.62.

### *Holoplatys meda* n.sp.

Fig.17, Map 2

**Material examined.** Western Australia: HOLOTYPE, female, Meda Station, 22 Aug. 1987, A.E. de Jong, WAMP 88/22; PARATYPE, female, South Hedland, at airport, under bark of *Eucalyptus* sp., 24 Apr. 1989, M.S. Harvey, WAMP 89/284.

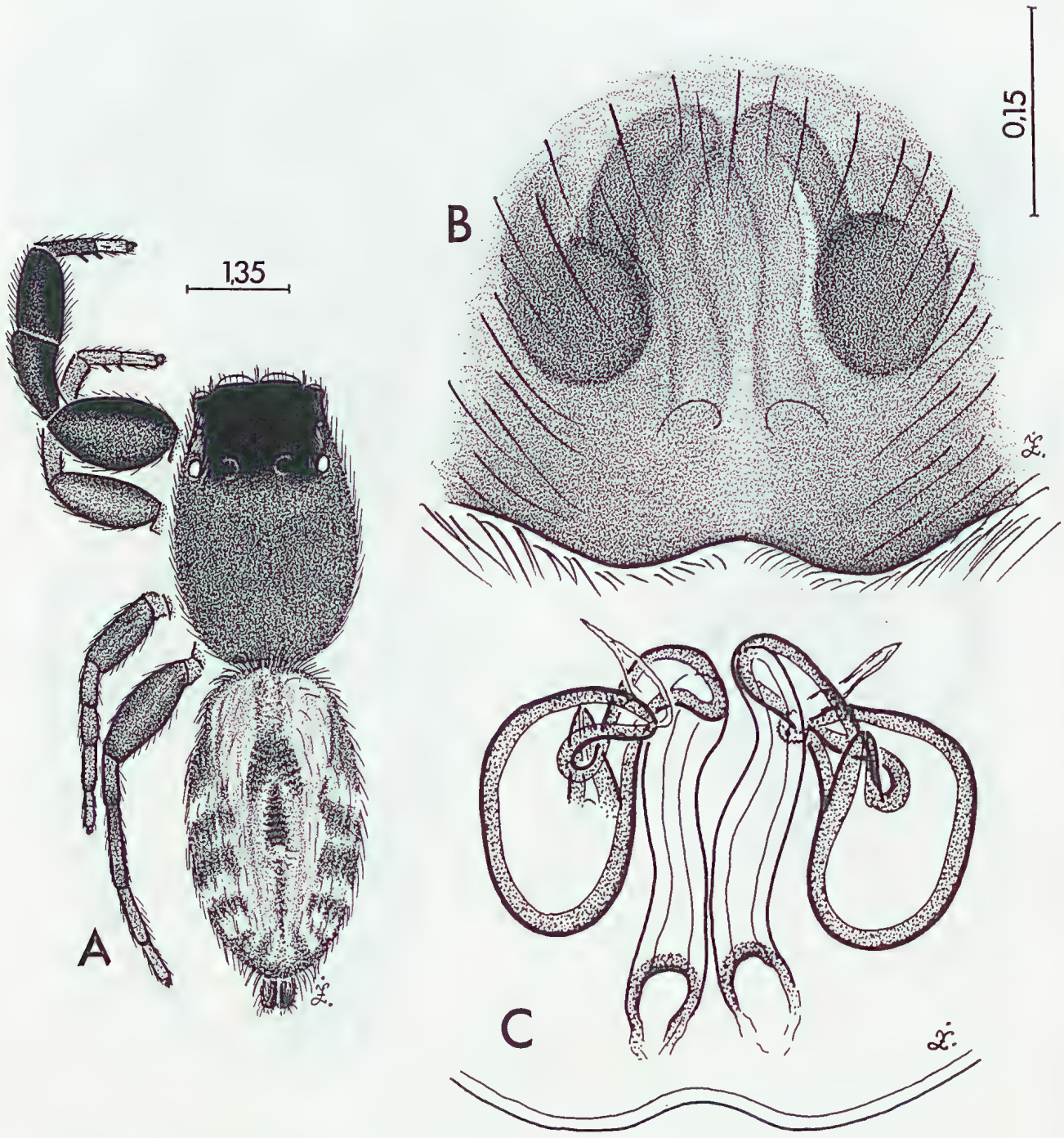



**Fig.17.** *Holoplatys meda*, female (holotype).

**Diagnosis.** Insemination ducts as in *rainbowi* but spermathecae relatively smaller, especially their distal parts. Also accessory glands in different position.

**Male.** The male is unknown.

**Female** (Fig.17A). Eye field black, thorax dirty-orange, marginally darker, with white and brown hairs. Abdomen with dark-grey and yellowish pattern, covered with white and brown hairs more numerous marginally. Spinnerets dirty-yellow. Clypeus black-brown with long white and blackish hairs. Chelicerae, maxillae and labium dark-brown, the last with yellow tips. Pedipalps dirty-orange, sternum dirty-brown, lighter posteriorly. Venter light-grey. Legs I brown, lighter distally and dorsoventrally. Other legs lighter.

Genitalia (Fig.17B,C) with long insemination ducts. Spermathecae smaller than in *rainbowi* and accessory glands on inner walls of spermathecae.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 3.56-3.75 (3.65), CW 2.27-2.60 (2.43), CW/CL 0.62-0.66 (0.64), EFL 1.12, EFL/CL 0.31-0.32 (0.31), AEW 1.65, PEW 1.71-1.75 (1.73), AL 3.96-5.04 (4.50).

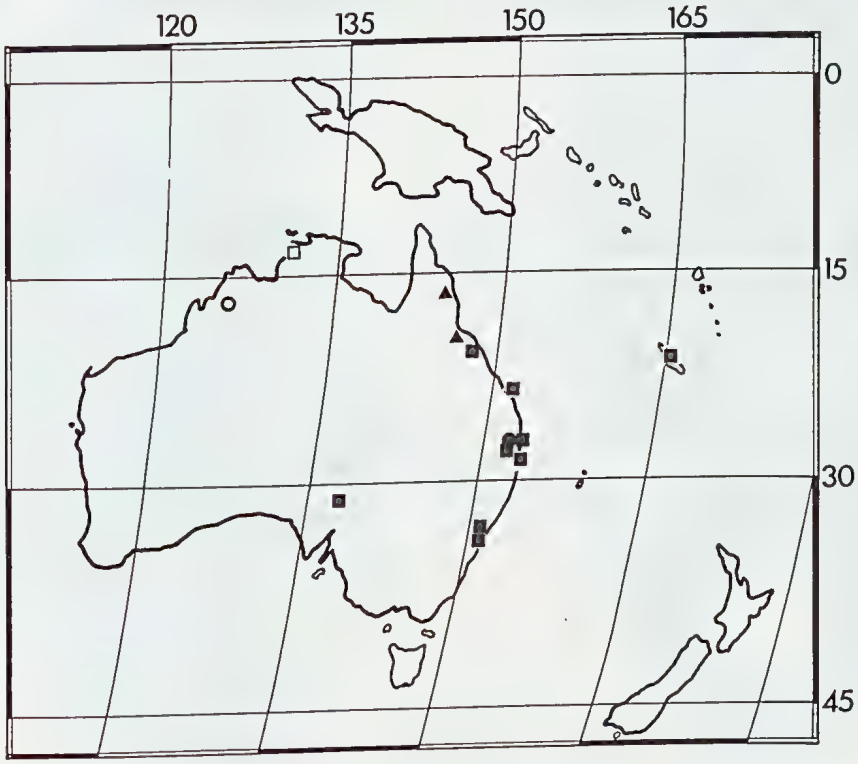
### *Holoplatys semiplanata* n.sp.

Figs 18-20, Map 3

**Material examined.** Queensland: HOLOTYPE, male, ALLOTYPE, female, PARATYPES, female, juvenile, Heron Island, heathland, under bark of dead wood, 15 July 1978, V. Davies, QMB S3580; female, Proserpine, 17 Aug. 1971, N.C. Coleman, QMB S4600; female, Brisbane, Mitchelton, 6 Dec. 1983, C. Morrow, QMB S4566; male, Lake Broadwater, buildings, 1-15 Nov. 1984, V. Wood, QMB S4599; female, Lake Broadwater, Surveyors Gully, under bark, 27 Nov. 1985, M. Bennie, V. Davies, QMB S3599; male, Ciba-Geigy, Beenleigh, 8 Nov. 1978, L. Thomas, QMB S4578. New South Wales: PARATYPES, male, Kyogle, ex mud cell of *Sceliphron sp.* (wasp), 16 Feb. 1984, D.J. Scambler, AMS KS18863; male, female, Botany, 20 Apr. 1980, R. Mascord, AMS KS7574; female, Ermington, 16 Mar. 1958, R. Ford, AMS KS18864; male, Sydney, Oxford Falls, 29 May 1984, D. Mead-Hunter, WAMP 88/36; male, Botany, 28 Mar. 1978, R. Mascord, AMS KS18862. South Australia: PARATYPES, male, Andamooka Range, Exp. camp 5.7, 3 Sept. 1947, Mitchell, G.F. Gross, SAMA N1988339. New Caledonia: PARATYPE, male, Noumea, 'Ringarsoma', 26 Sept. 1901, J.J. Walker, AMS KS18861.

**Diagnosis.** Similar to *complanata* but embolus shorter, tegulum more elongate, accessory glands shorter and straight. In comparison to other males of the group abdominal pattern different.

**Male** (Fig.18A). White hairs along median and marginal parts of dark-brown cephalothorax. Abdomen with anterior orange scutum and dark-grey and light pattern. Spinnerets dark-grey to black. Clypeus grey to black with single long hairs of the same colour. Chelicerae brown with fringe of white hairs on frontal surface. Maxillae brown to black with lighter tips, labium and sternum dirty-brown. Venter dark-grey with




Map 3. Open square – *H. kempensis* n.sp.; closed triangle – H. *oakensis* n.sp.; closed circle – *H. rainbowi* n.sp.; closed square – *H. semiplanata* n.sp.; open circle – *H. windjanensis* n.sp.

2 longitudinal lighter stripes. Legs brown, lighter distally, darker on tibia and lateral surfaces of other segments.

Palpal organ (Fig.18B,C) similar to other species - especially to *colemani*.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1. r0-1.

*Dimensions.* CL 2,97-4,48 (3.44), CW 1.91-2.57 (2.13), CW/CL 0.57-0.64 (0.62), EFL 0.92-1.13 (1.01), EFL/CL 0.25-0.30 (0.29), AEW 1.41-1.65 (1.46), PEW 1.41-1.71 (1.50), AL 3.36-5.34 (4.01).

**Female** (Figs 19A, 20A). Dorsal aspect as in male, but no abdominal scutum. Chelicerae, maxillae, labium and legs as in male, but the first not fringed. Pedipalps orange-brown, sternum light-brown with darker margin.

Genitalia (Figs 19B,C, 20B,C) similar to *complanata* but accessory glands shorter, not curved.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r0-1.

*Dimensions.* CL 3.56-4.03 (3.79), CW 2.24-2.51 (2.39), CW/CL 0.62-0.64 (0.63), EFL 1.05-1.28 (1.15),

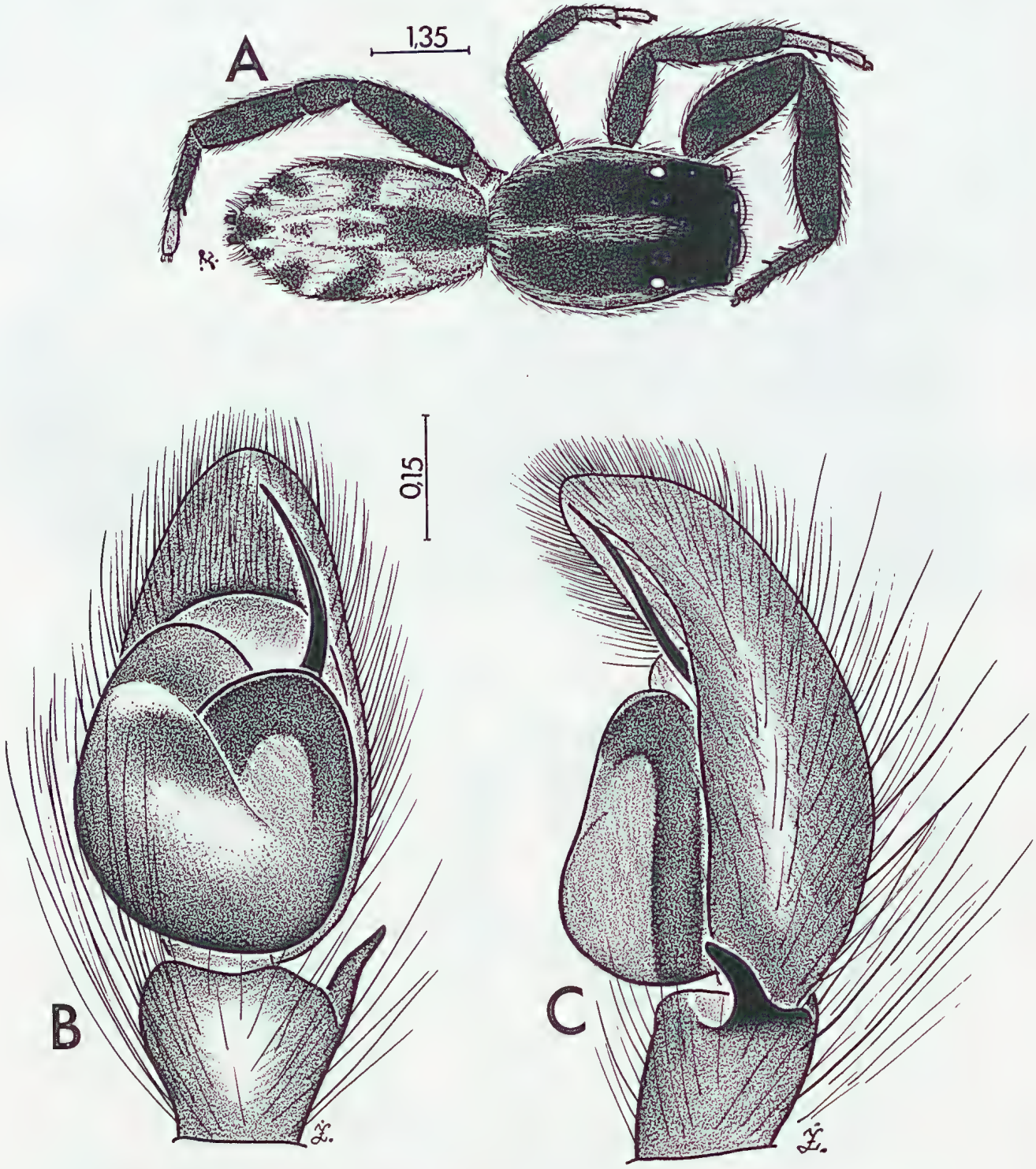



**Fig.18.** *Holoplatys semiplanata*, male (holotype).

EFL/CL 0.28-0.32 (0.30), AEW 1.58-1.75 (1.65), PEW 1.65-1.78 (1.70), AL 4.35-7.26 (5.49).

### *Holoplatys oakensis* n.sp.

Fig.21, Map 3

**Material examined.** Queensland: HOLOTYPE, female, Oak Forest, summer 1971-72, N.C. Coleman, QMB S4570; PARATYPE, female, Mount Elliot N.P., Alligator Creek, July 1986, M.S. Harvey, P.J. Vaughan, WAMP 89/269.

**Diagnosis.** Genitalic structure similar to *semiplanata* but body colour much lighter, cephalothorax with numerous lateral white hairs, abdominal median stripe less distinctive.

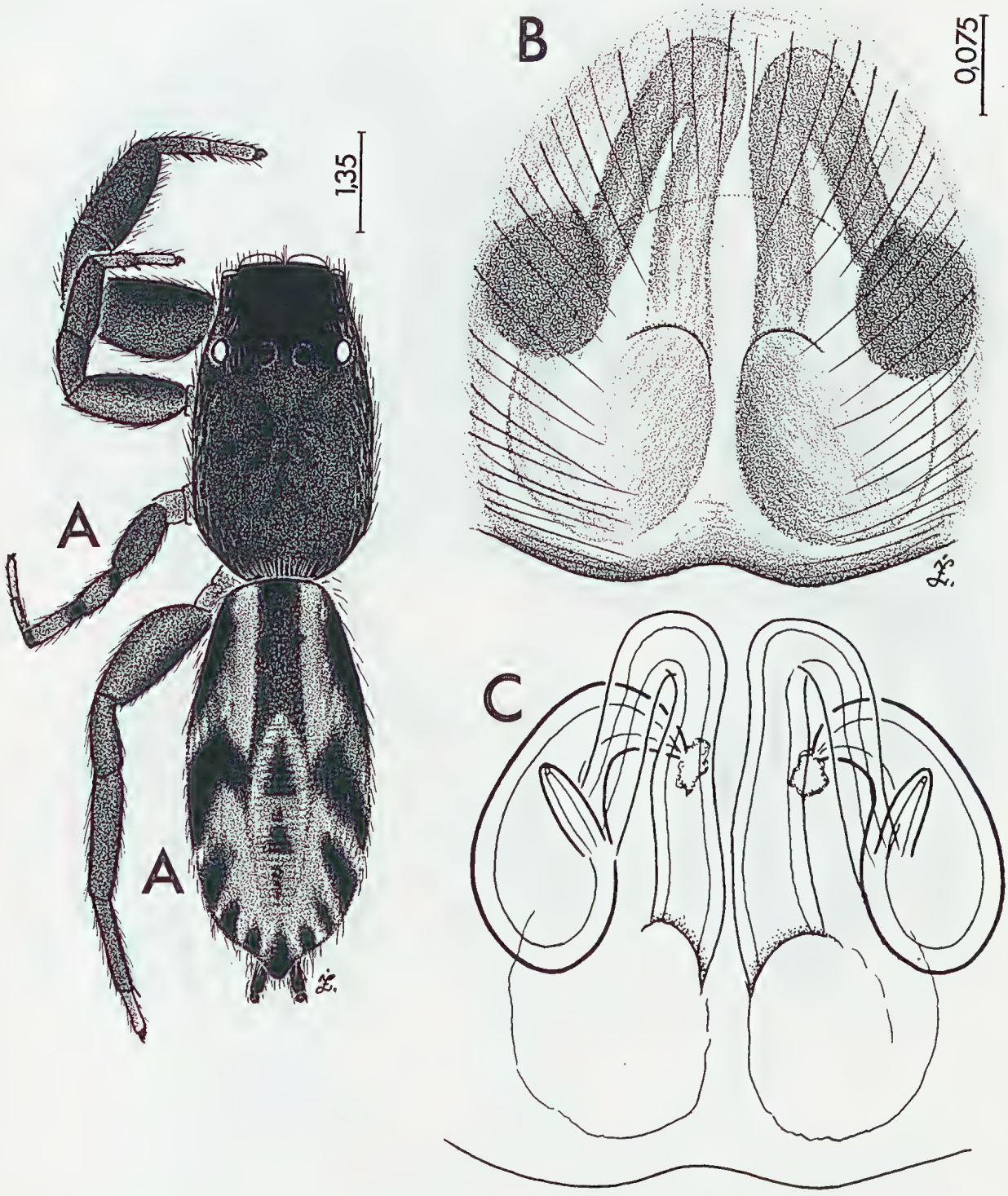



**Fig.19.** *Holoplatys semiplanata*, female (allotype).

**Male.** The male is unknown.

**Female** (Fig.21A). Eye field black, thorax brown with marginal stripes of white hairs. Abdomen with yellow and beige pattern but generally lighter than in other species of the group. Spinnerets yellow. Clypeus black, chelicerae, maxillae, labium and sternum dirty-brown, pedipalps yellow. Venter yellowish. Legs I brown, others yellow.

Genitalia (Fig.21B,C) very similar to *semiplanata*.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.80-3.10 (2.95), CW 1.80-1.98, CW/CL 0.58-0.63 (0.61), EFL 0.93-0.99 (0.96), EFL/CL 0.31-0.33 (0.32), AEW 1.35-1.45 (1.40), PEW 1.41-1.49 (1.45), AL 3.84-3.89 (3.86).

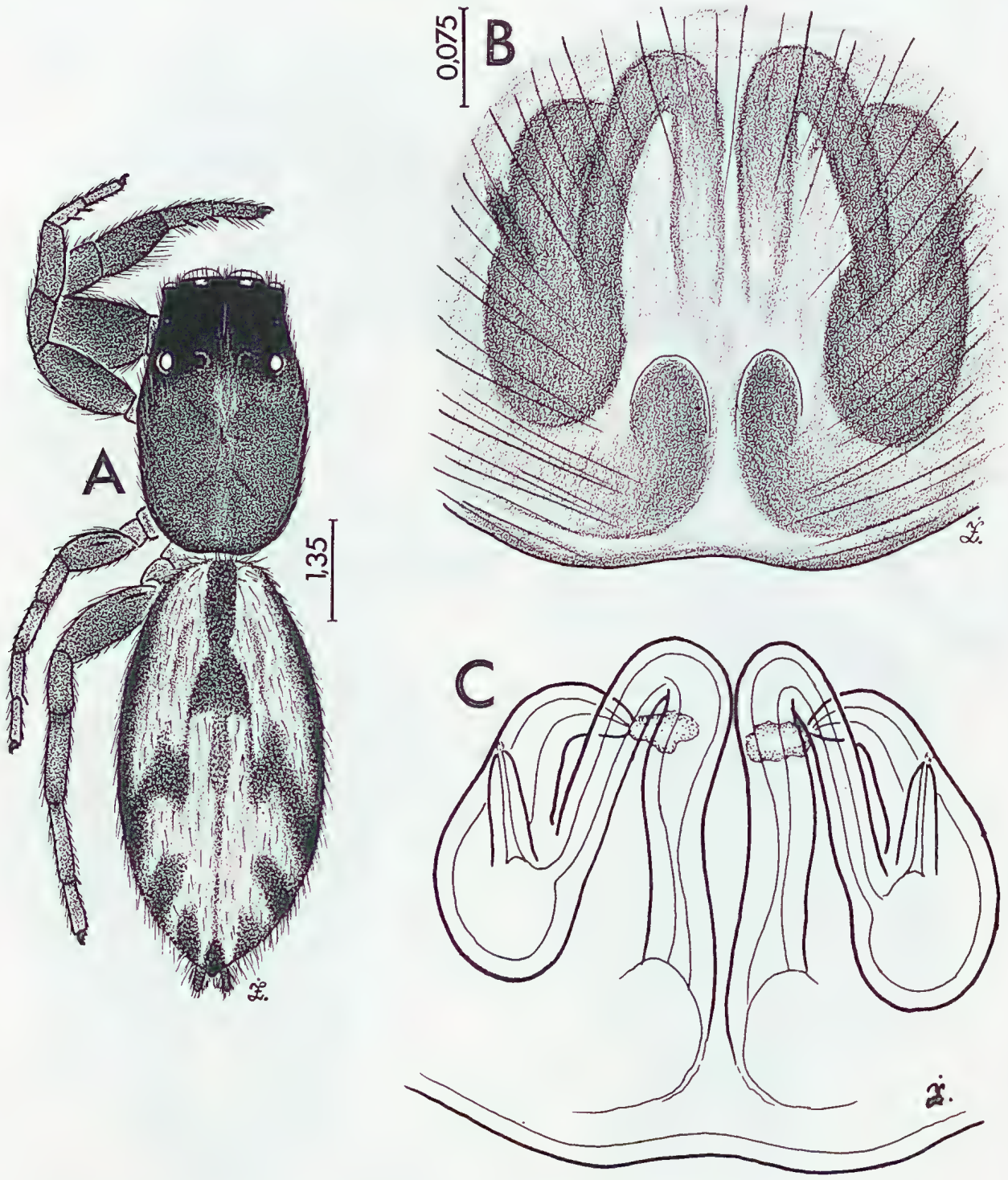



**Fig.20.** *Holoplatys semiplanata*, female (paratype from Brisbane).

### *Holoplatys kempensis* n.sp.

Fig.22, Map 3

**Material examined.** Northern Territory: HOLOTYPE, female, PARATYPES, 2 juveniles, Kemp Airstrip, bark peeling, 16 Nov. 1979, R. Raven, QMB S3589.

**Diagnosis.** Abdomen with white pigmented spots on beige background. Body size smaller than in other representatives of the group, depressions on eye field missing.

**Male.** The male is unknown.

**Female** (Fig.22A). Eye field dark-grey, eye surrounding darker, thorax yellow, its lower margin darker. Abdomen with beige median stripe furced posteriorly and with white pigmented spots on beige background. Abdominal margin blackish. Spinnerets yellowish. Clypeus dark, brown-grey. Chelicerae, maxillae, labium, sternum and legs yellow. Venter with white pigmented spots as dorsally.

Genitalia (Fig.22B,C) similar to other species of the group.

*Leg spination.* mI: p1-1; mII: p0-1.

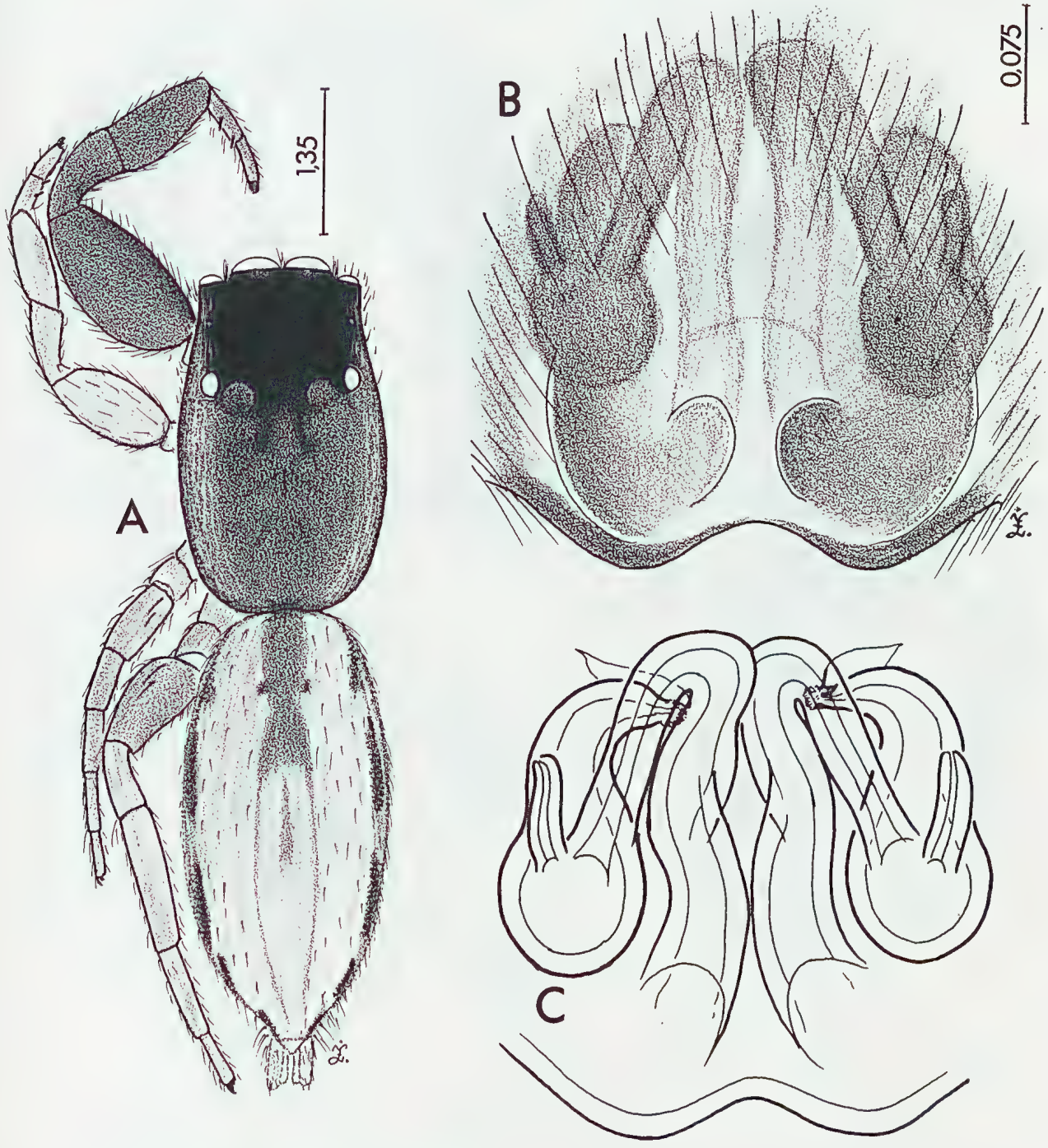



**Fig.21.** *Holoplatys oakensis*, female (holotype).

*Dimensions*. CL 2.51, CW 1.59, CW/CL 0.63, EFL 0.84, EFL/CL 0.34, AEW 1.25, PEW 1.25, AL 3.03.

### *Holoplatys windjanensis* n.sp.

Fig.23, Map 3

**Material examined.** Western Australia: HOLOTYPE, female, Windjana Gorge, 21 Aug. 1987, A.E. de Jong, WAMP 88/34.

**Diagnosis.** Abdomen with dark median hairs and white pigmented spots like in *kempensis* but tibial spines on legs I present.

**Male.** The male is unknown.

**Female** (Fig.23A). Eye field brownish-grey with light-

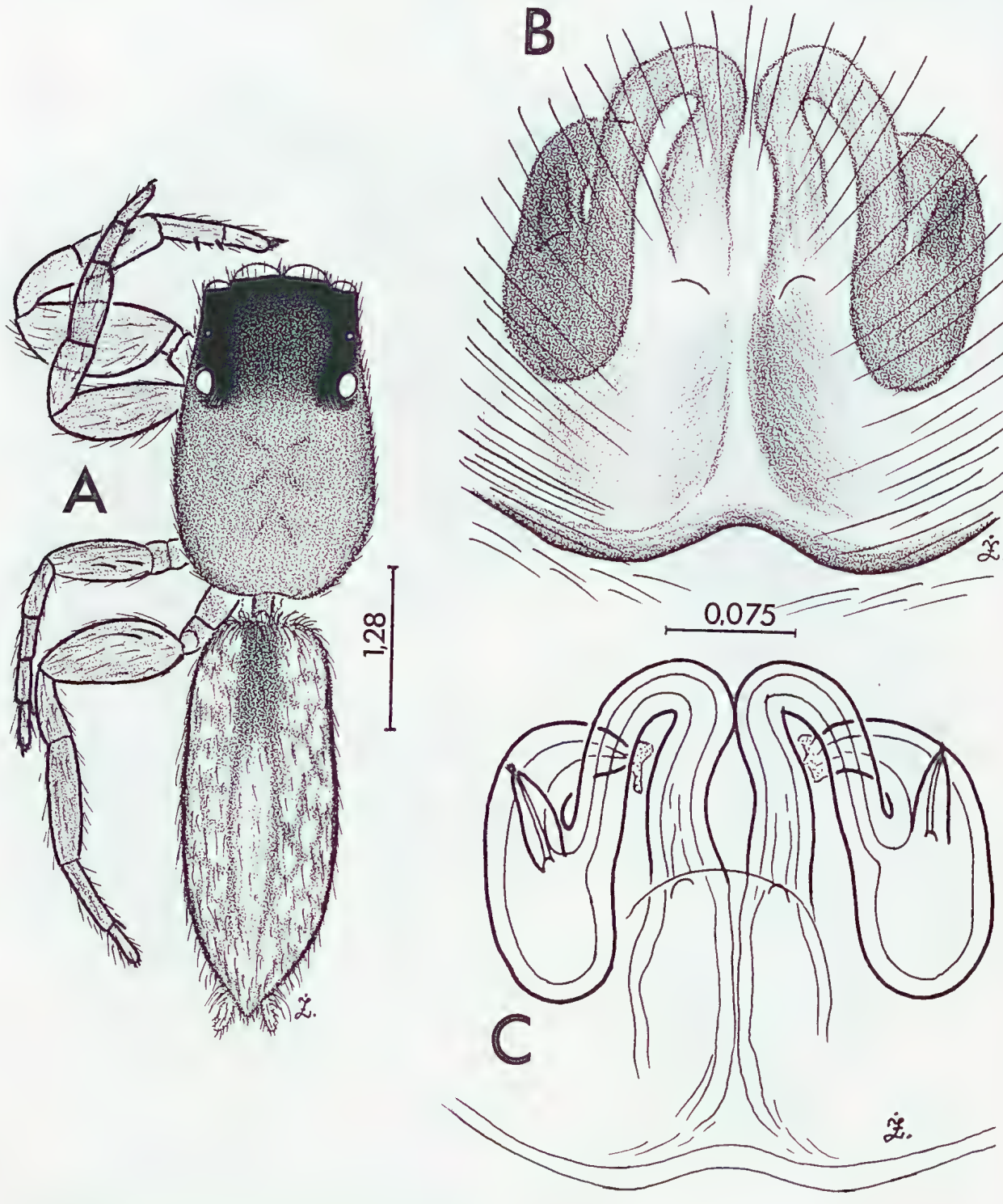



**Fig.22.** *Holoplatys kempensis*, female (holotype).

grey hairs in its central part. Surroundings of eyes black. Thorax with yellow median stripe surrounded by dark hairs. Lower margin of cephalothorax brown. Abdomen with median black hairs and white pigmented spots on pale background. Lateral surfaces with dark-grey hairs. Clypeus dark-brown, fringed with white hairs. Chelicerae dirty-brown, pedipalps yellowish, with white long hairs. Maxillae and labium grey-orange, sternum yellow with darker margin. Venter spotted as dorsally. Legs yellowish.

Genitalia (Fig.23B,C). Insemination ducts, spermathecae and accessory glands shorter than in other species of the group.

*Leg spination.* tI: p1-1; mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 3.17, CW 2.18, CW/CL 0.68, EFL 1.05, EFL/CL 0.33, AEW 1.52, PEW 1.58, AL 4.22.

## The *planissima* Group

The group consists of eight species, spread from tropical Queensland through New South Wales to Western Australia. Body small to medium (4.21-8.11 mm). Abdomen usually with dark medium stripe or herring-bone pattern. No tibial spines on legs I and II. Male palpal organ with dorsal and lateral tibial apophyses, tegulum large, sac-like, embolus shorter and more massive than in the *complanata* group. Epigynal depression usually with distinctive margins. Species included: *planissima, strzeleckii, tasmanensis, fusca, pemberton, marscordi, braemarensis, julimarina.*

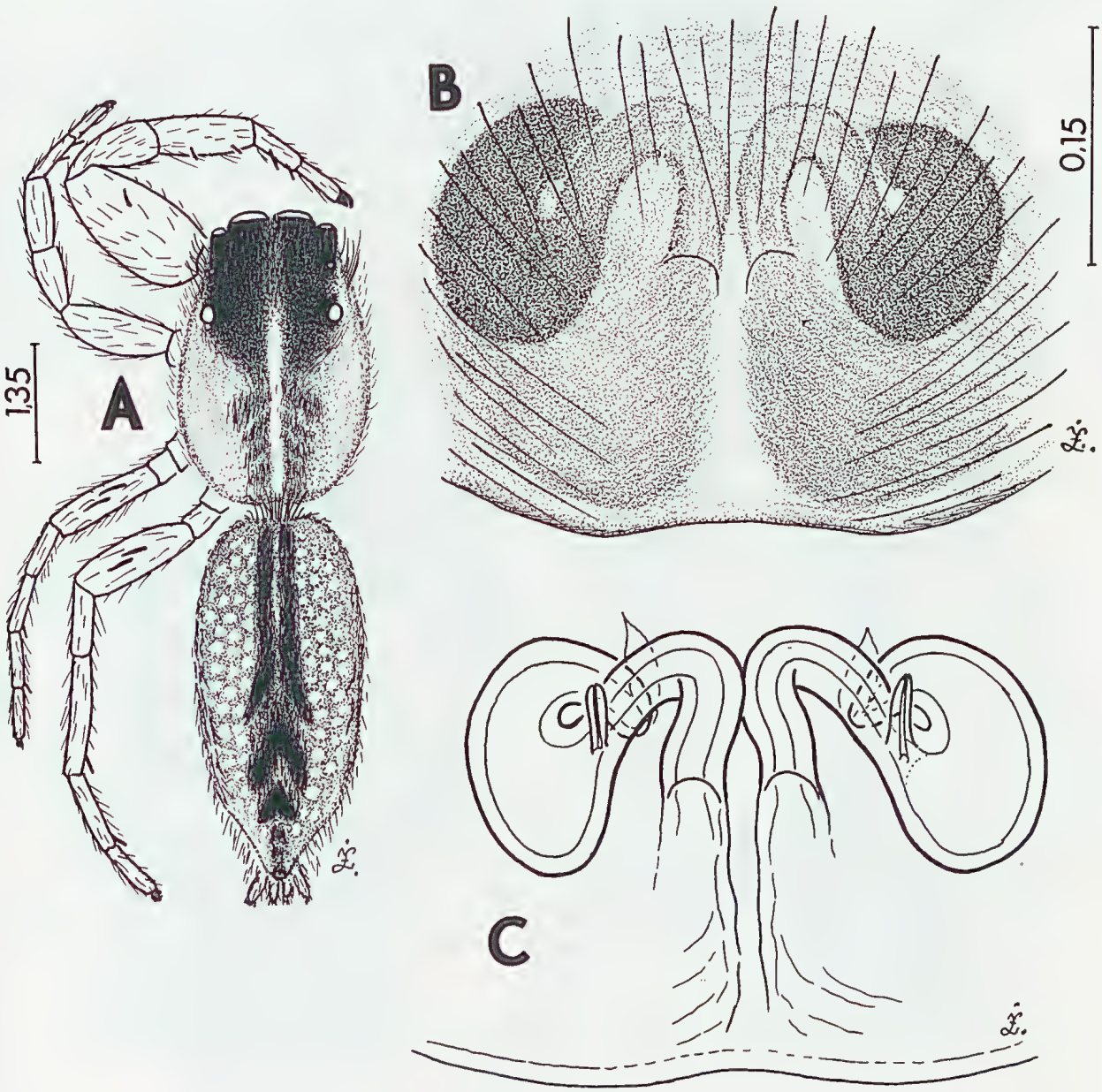



**Fig.23.** *Holoplatys windjanensis*, female (holotype).

### *Holoplatys planissima* (L. Koch)

Figs 24-27, Map 4

*Marptusa planissima* L. Koch, 1879: 1100
*Holoplatys planissima*.–Simon, 1885: 445.–Mascord, 1970: 28.–Prószynski, 1984: 51.–Davies & Zabka, 1989: 262.

**Material examined.** Queensland: SYNTYPES, male, female, Rockhampton, ZMB 3488; female, Cairns, N.C. Coleman, 25 May 1969, AMS KS18879; female, Girraween, R.R. Jackson, 8 Sept. 1983, QMB S3562; 9 males, 20 females, 7 juveniles, Lake Broadwater, 21 Mar. 1984, 11 July 1984, 28 July 1984, 17 Oct. 1984, 16 Nov. 1984, 26 Nov. 1984, 26-27 Jan. 1985, M. Bennie, V. Davies, J. Gallon, P. Lawless, QMB S3595-6, S3600-7; female, Salvator Rosa N.P., 13 Sept. 1984, M. Bennie, QMB S3549. New South Wales: female, Antonio, near Rydal, 18 Jan. 1906, L.J.H. Morian, AMS KS18881; 2 females, Jenolan Caves, Y. Wiburd, AMS KS18878; female, south of Wilcannia, Tintinology Station, Darling River banks, under bark, 6 Apr. 198, D. Hirst, SAMA N1988355; male, female, East Kurrajong, 23 July 196, R. Mascord, AMS KS18876; 2 females, Sydney, 18 Feb. 1899, A. Rainbow, AMS KS 18880; 2 females, Silverdale, 2 July 1967, C.E. Chadwick, AMS KS1. Victoria: female, 17 km east of Bendigo, 17 Nov. 1976. G. Daniels, AMS KS6; female, 8.5 km south of Mount Killawara, Warby Ranges, under *Eucalyptus* bark, Nov. 1978, M.S. Harvey, WAMP 89/279; female, 32 km north-west of Stawell, on Western Highway, under bark of *Eucalyptus* sp., 30 June 1982, M.S. Harvey, B.E. Roberts, WAMP 89/280. South Australia: 5 females, 5 km south of Mylor, 8 June 1980, A.D. Austin, AMS KS10527. Western Australia: 2 females, 4 juveniles, Kalgoorlie, Mar. 1968, WAMP 88/14, 88/17-20.

**Diagnosis.** Body colour shows some individual variability. Leg I long, especially tibia and metatarsus of male, abdominal anterior scutum more or less visible. Clypeus not fringed. Genitalia almost identical to many other species of the group.

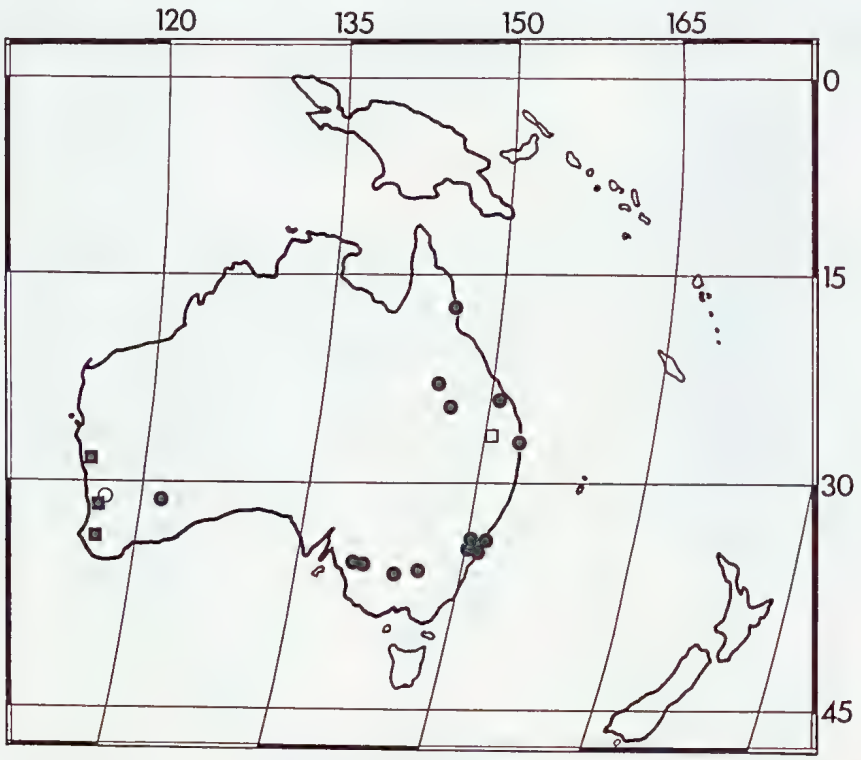
**Male** (Figs 24A, 26A). Cephalothorax brown to black, darker on eye field. Marginally white hairs present. Abdomen dark with anterior scutum and white lateral hairs. Spinnerets grey to black. Clypeus, chelicerae, maxillae, labium and sternum grey-brown to black, venter light to dark-grey. Legs long, especially first ones, brown to black, darker laterally and around joints.

Palpal organ (Figs 24B,C, 26B,C) with crescent-like embolus and sac-like tegulum with shallow depression on its surface.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.44-3.10 (2.74), CW 1.45-1.91 (1.69), CW/CL 0.59-0.61 (0.60), EFL 0.73-0.86 (0.80), EFL/CL 0.27-0.30 (0.29), AEW 1.05-1.25 (1.14), PEW 1.05-1.32 (1.17), AL 3.10-4.62 (3.71).

**Female** (Figs 25A, 27A,E). Cephalothorax similar to that in male but slightly wider, also marginal white hairs less numerous. Abdomen beige with darker median pattern and lighter longitudinal stripes. Sometimes abdomen much darker. Clypeus, chelicerae, labium, sternum and venter as in male, pedipalps orange to brown. Legs coloured as




Map 4. Open square – *H. braemarensis* n.sp.; open circle – *H. julimarina* n.sp.; closed square – *H. pemberton* n.sp.; closed circle – *H. planissima* (L. Koch).

in male but first ones considerably shorter.

Genitalia (Figs 25B,C, 27B-D) with large spermathecae and relatively long insemination ducts.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.83-3.63 (3.22), CW 1.65-1.98 (1.82), CW/CL 0.54-0.61 (0.58), EFL 0.79-0.89 (0.83), EFL/CL 0.23-0.29 (0.26), AEW 1.14-1.44 (1.29), PEW 1.14-1.48 (1.31), AL 4.35-4.81 (4.58).

### *Holoplatys strzeleckii* n.sp.

Figs 28-29, Map 5

**Material examined.** South Australia: HOLOTYPE, male, ALLOTYPE, female, PARATYPES, juvenile, 5 km south of Mylor, 20 Jan. 1980, A.D. Austin, QMB S3585; 2 females, Mylor, 18 June 1979, QMB S3575, S3577; female, 5 km south of

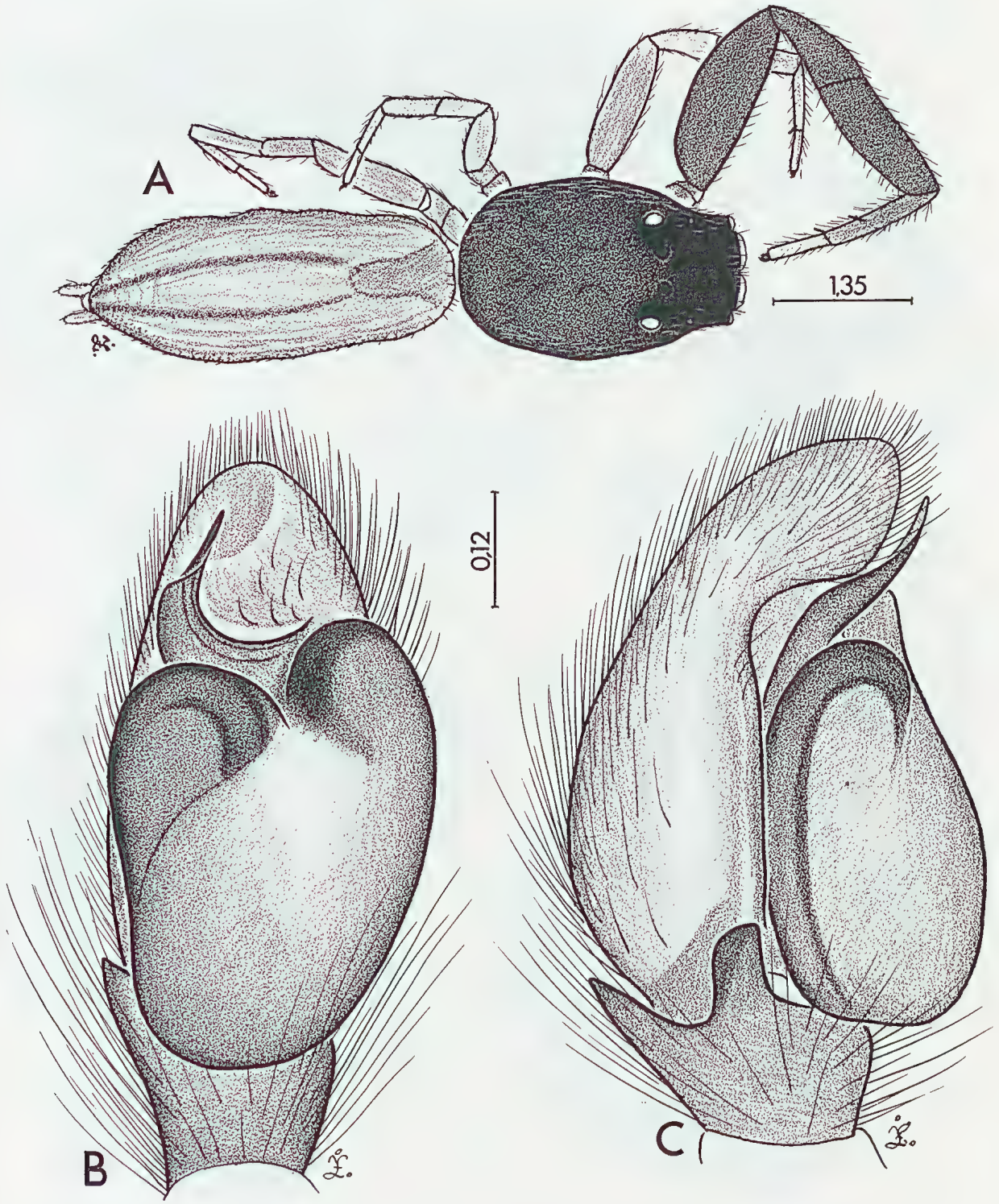



**Fig.24.** *Holoplatys planissima*, male (syntype).

Mylor, 8 June 1980, A.D. Austin, AMS KS10527; 3 females, same data, AMS KS19452; 3 females, 3 km south of Mylor, 20 Jan. 1980, A.D. Austin, QMB S3590; 2 females, Snow Gum Reserve, Caroline Forest, under *Eucalyptus* bark, 20 Apr. 1979, D. Lee, SAMA N1988343-4; 3 females, Roachdale Natural Trust Reserve, near Williamstown, 8 Aug. 1980, J.J.H., M.L. Szent-Ivany, SAMA N1988345-7; female, Sellicks-Aldinga Scrub, under bark, 15 Sept. 1987, D. Hirst, SAMA N1988341; female, Kangaroo Island, Rocky River Waterhole, 3-4 Dec. 1982, J. Pennington, M. Bennett, SAMA N1988342; female, Lofty Range Mountains, Loftia Park, under bark of *Eucalyptus*, 25 Mar. 1984, R.V. Southcott, SAMA N1988340.

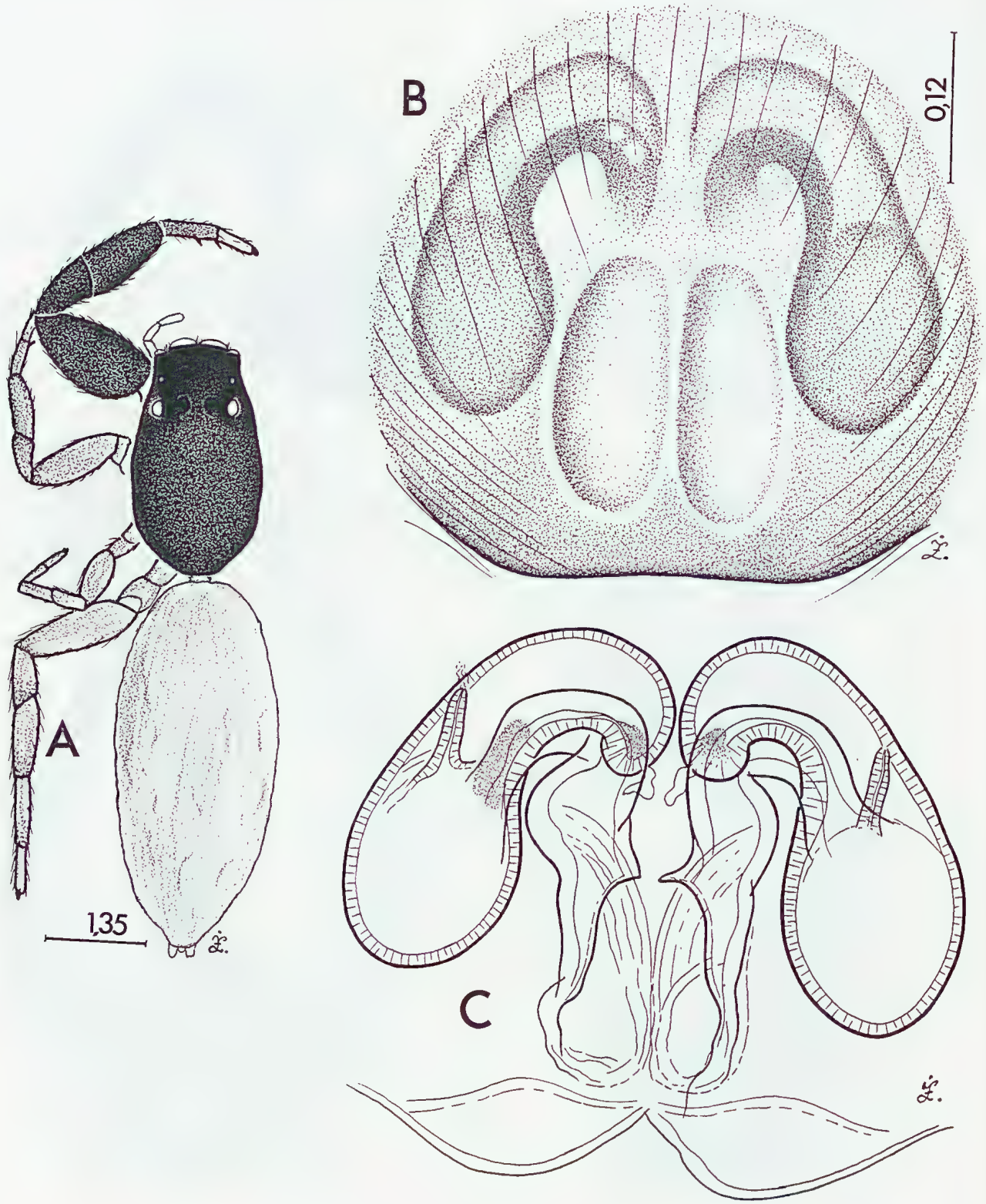



**Fig.25.** *Holoplatys planissima*, female (syntype).

Tasmania: PARATYPE, male, Devonport, 18 Feb. 1983, A. Webber, TMH J195.

**Etymology.** The specific name is proposed in honour of Polish naturalist and explorer John Paul Strzelecki.

**Diagnosis.** Dark abdominal stripe very distinctive, numerous white hairs on lateral surfaces of cephalothorax, tegulum with well marked depression.

**Male** (Fig.28A). Eye field black-brown, thorax brown. Marginally numerous white hairs. Abdomen with anterior scutum and dark median stripe on beige background. Spinnerets grey-brown. Clypeus black with white hairs. Chelicerae dirty-orange, maxillae,

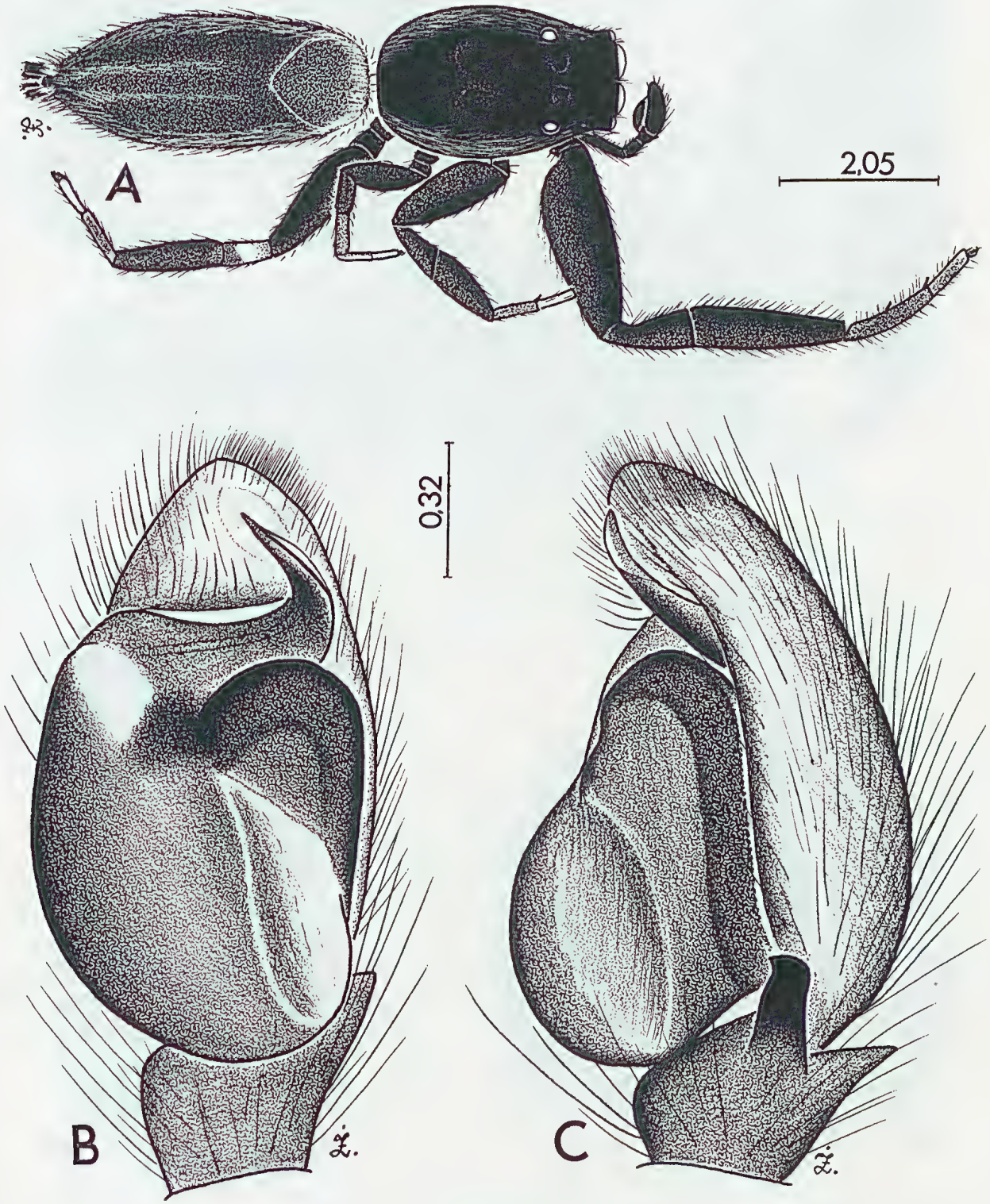



**Fig.26.** *Holoplatys planissima*, male from Lake Broadwater.

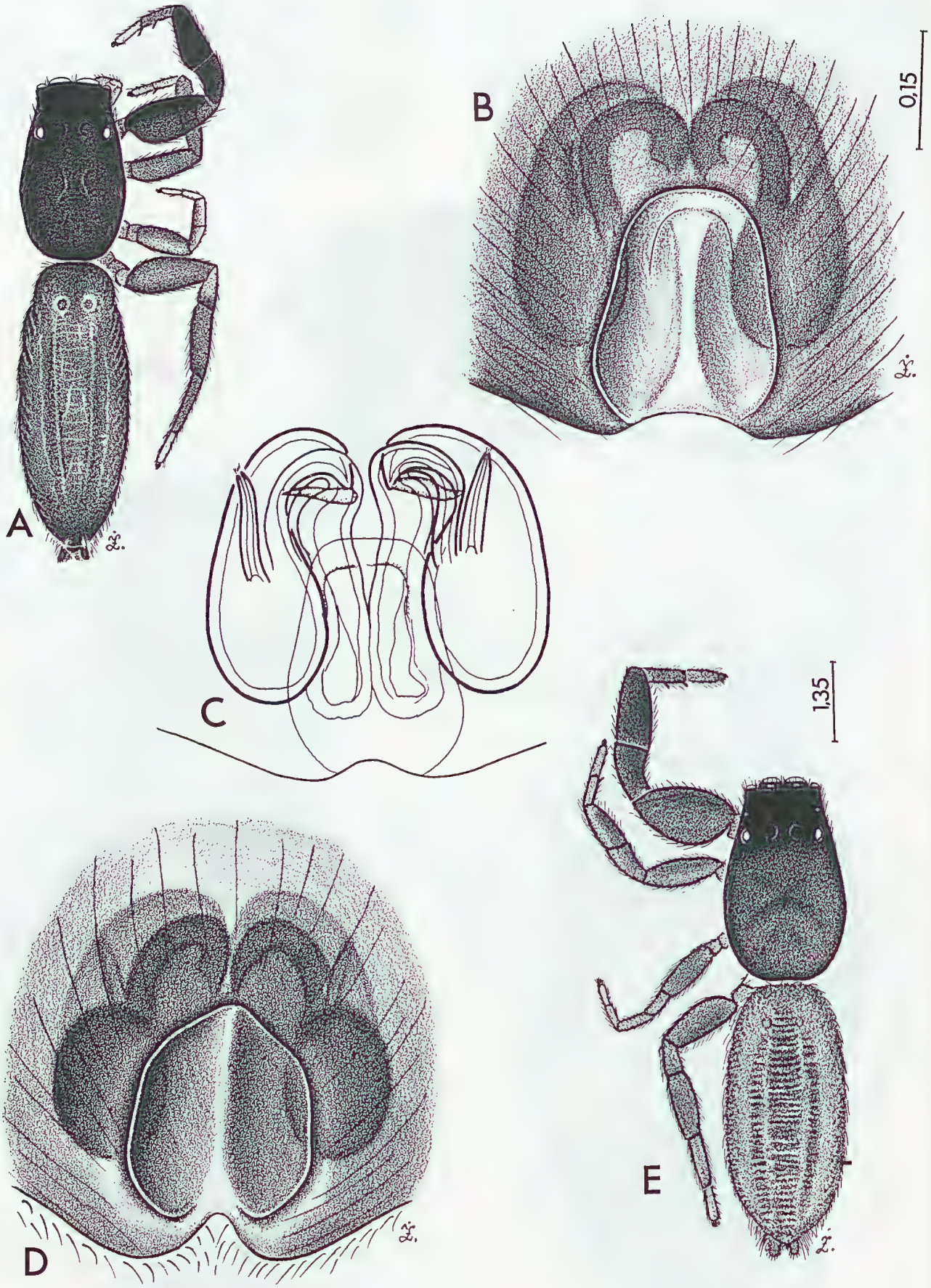



**Fig.27.** *Holoplatys planissima*, females from Lake Broadwater.

labium and sternum dark-orange. Venter beige centrally, darker laterally. Legs I long, brown, other legs slightly lighter.

Palpal organ (Fig.28B,C) very similar to *planissima* but depression on tegulum surface better marked.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.31-2.57 (2.44), CW 1.51-1.83 (1.67), CW/CL 0.65-0.71 (0.68), EFL 0.73-0.79 (0.76), EFL/CL 0.31, AEW 0.99-1.12 (1.05), PEW 1.12-1.15 (1.13), AL 2.90-3.30 (3.10).

**Female** (Fig.29A). Cephalothorax coloured as in male. Abdomen with dark central and lateral pattern. The rest grey to beige. Clypeus dark-grey to black with single dark hairs. Chelicerae brown. Maxillae and labium dirty-brown with lighter tips, sternum dirty-orange to brown with darker edges. Venter beige to grey. Leg I brown, lighter dorsoventrally and distally, other legs slightly lighter.

Genitalia (Fig.29B,C) very similar to *planissima* but depression of epigyne less distinctive.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.77-3.43 (3.05), CW 1.85-2.18 (2.00), CW/CL 0.61-0.65 (0.64), EFL 0.79-0.92 (0.86),

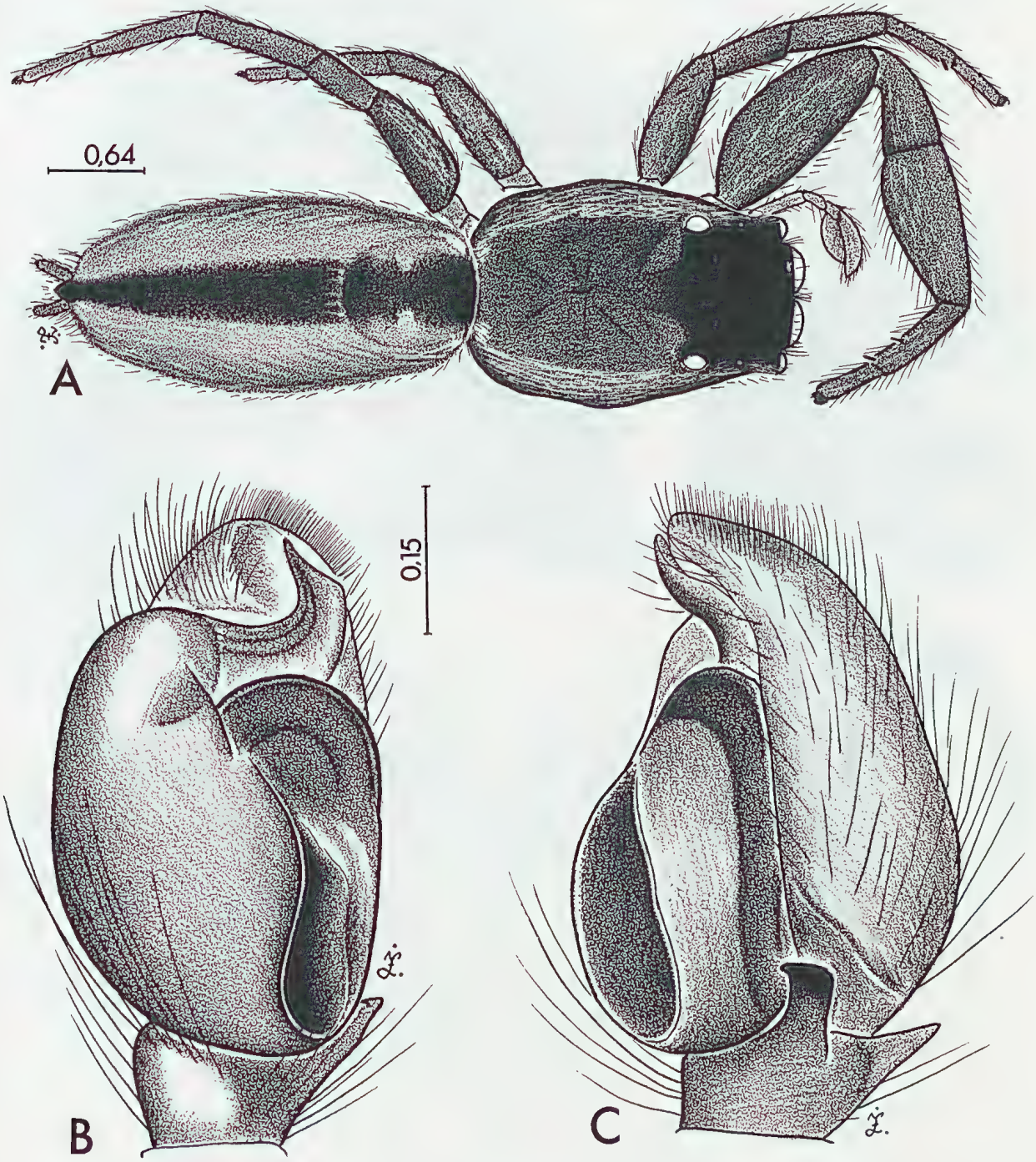



**Fig.28.** *Holoplatys strzeleckii*, male (paratype) from Mylor area.

EFL/CL 0.26-0.31 (0.28), AEW 1.13-1.33 (1.23), PEW 1.22-1.45 (1.34), AL 4.22-4.68 (4.37).

### *Holoplatys tasmanensis* n.sp.

Fig.30, Map 5

**Material examined.** Tasmania: HOLOTYPE, female, Andrew River, peeling bark of tea tree, 23 Mar. 1988, M. Gray, AMS KS19315; PARATYPES, 2 juveniles, same data, AMS KS19316.

**Diagnosis.** Species closely related to *strzeleckii* but dark abdominal stripe less distinctive, clypeus fringed, and accessory glands much shorter.

**Male.** The male is unknown.

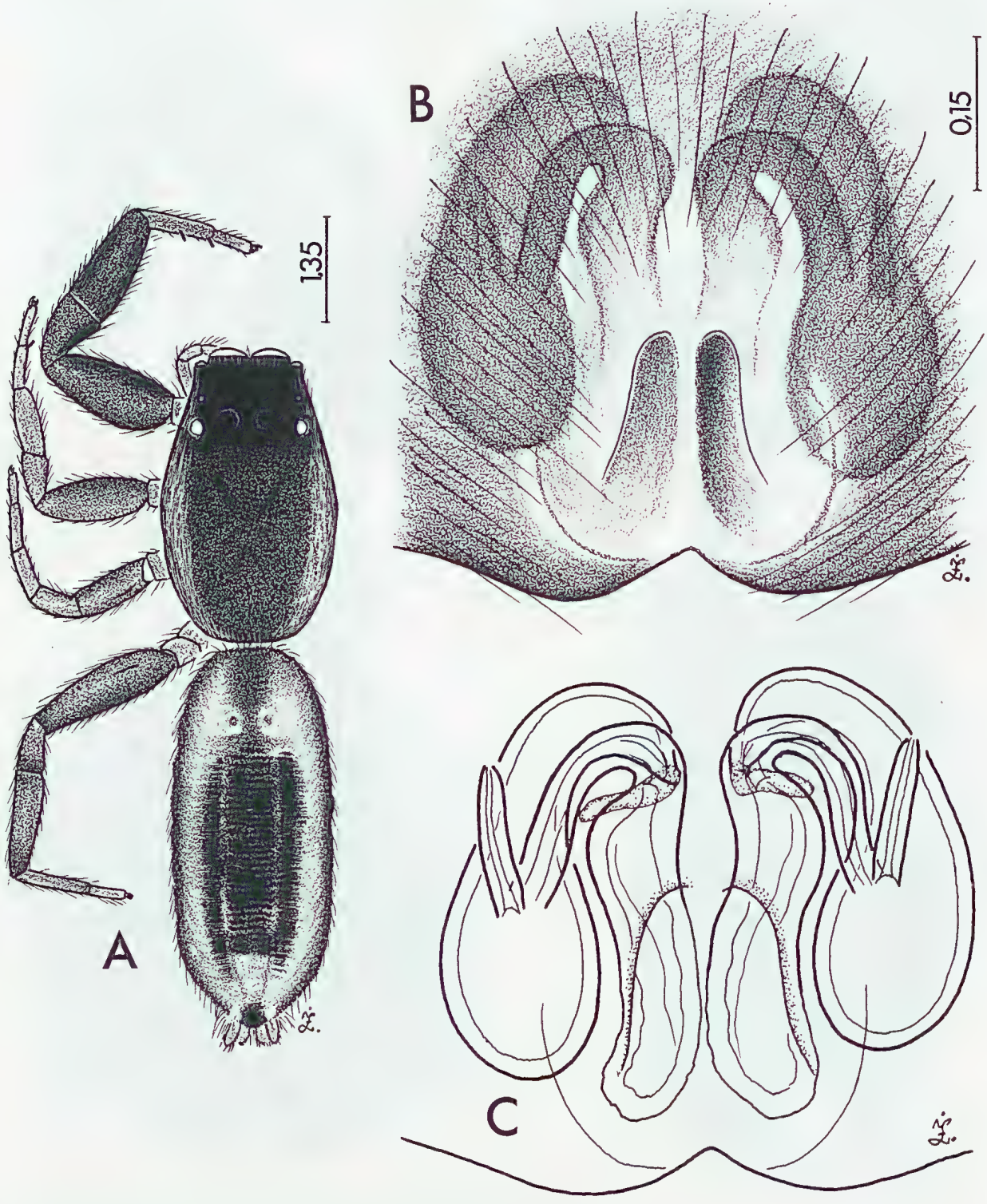



**Fig.29.** *Holoplatys strzeleckii*, female (allotype).

**Female** (Fig.30A). Eye field black. Thorax dirty light-brown medially, laterally lighter with white hairs. Abdomen yellowish with dark-grey median belt. Spinnerets yellow-grey. Clypeus blackish, fringed with short white hairs. Chelicerae dark-brown, maxillae and labium brown, the first with light tips. Labium brownish, sternum dirty-brownish. Venter yellow. Legs I laterally brown, dorsoventrally lighter. Other legs yellow.

Genitalia (Fig.30B,C) similar to related species. Spermathecae rather elongated, accessory glands thin.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.70, CW 1.71, CW/CL 0.63, EFL 0.79, EFL/CL 0.29, AEW 1.15, PEW 1.18, AL 4.45.

***Holoplatys fusca*** (Karsch) n.comb.

Figs 31-34, Map 5

*Marpissa fusca* Karsch, 1878: 28.
*Ocrisiona fusca.*–Rainbow, 1911: 291.

**Material examined.** New South Wales: SYNTYPE, male,

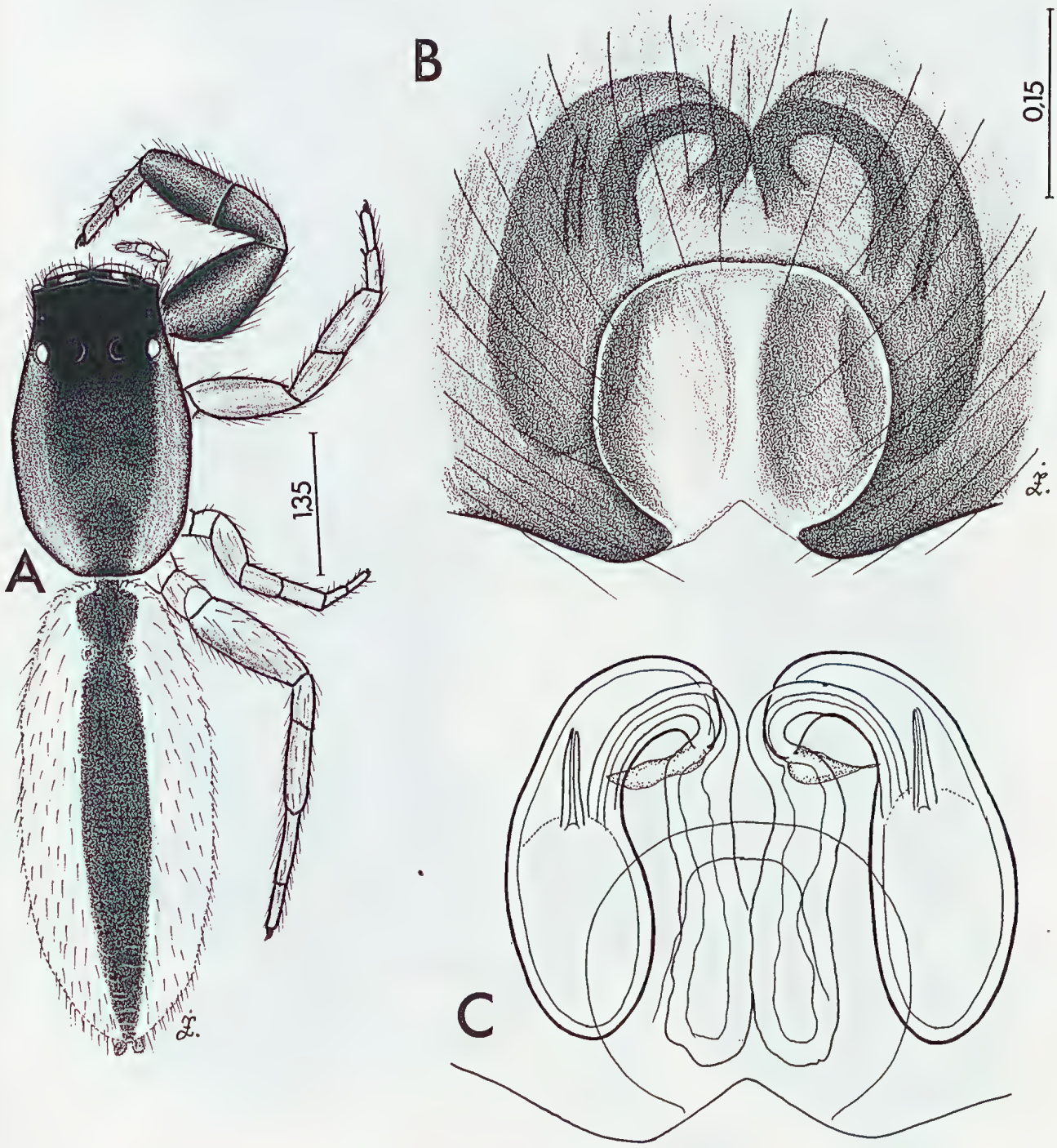



**Fig.30.** *Holoplatys tasmanensis*, female (holotype).

ZMB 1620. Queensland: 2 females, Brisbane, Rochedale State Forest, beating, bark, 2-17, 31 Jan. 1980, V. Davies, R. Raven, QMB S3552, S3557. South Australia: male, Cleland N.P., off flowering plants, 7 Oct. 1975, G. Crook, P. Christie, SAMA N1988351; 2 females, Roachdale Natural Trust Reserve, near Williamstown, 9 Aug. 1980, J.J.H., M.L. Szent-Ivany, SAMA N1988348-9: female, Marble Hill, under *Eucalyptus* bark with egg sac, 19 Nov. 1978, A.F. Lees, SAMA N1988350; female, 5 km south of Mylor, 8 June 1980, A.D. Austin, AMS KS10527; male, Kangaroo Island, Flinders Chase, from side of Rocky River along Shackles Road, 2[illegible] Mar. 1979, W. Zeidler, A. Gackle, SAMA N1988354; female Kangaroo Island, Ravine de Casoars, 6 Nov. 1987, D. Hirst SAMA N1988353; male, Kangaroo Island, 10-15 Jan. 1986 O.F. Clarke, SAMA N1988352. Western Australia: female juvenile, Lake Indoon, under *Eucalyptus* bark, 20 Sept. 1988 M. Zabka, WAMP 88/2384-5; female, Mundaring Weir IV.1963, J. Dell, WAMP 88/26; female, Moons Crossing Warren River, site 34, beneath Karri bark, 27 Jan. 1986 (FS4) G. Harold, WAMP 89/305.

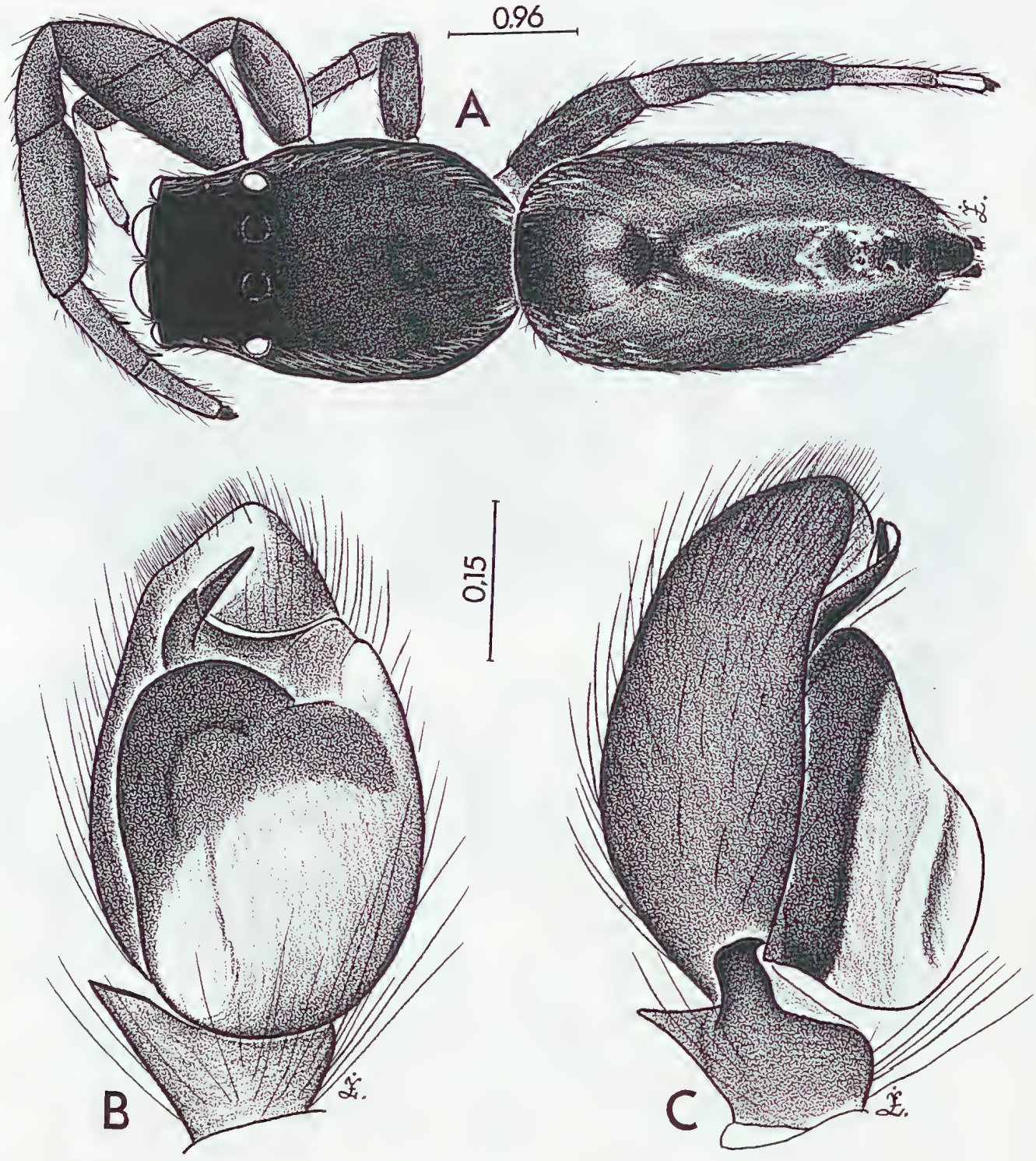



**Fig.31.** *Holoplatys fusca*, male (syntype).

**Diagnosis.** Species can be recognised by leg spination, fringed clypeus in both sexes and shape of lateral tibial apophysis.

**Male** (Fig.31A). Eye field brown-black, thorax brown, marginally darker with white hairs. Abdomen dark, with anterior scutum, central herring-bone pattern and white marginal hairs. Clypeus black-brown with fringe of short white hairs. Chelicerae brown with transverse stripe of white hairs. Maxillae and labium brown, sternum lighter,

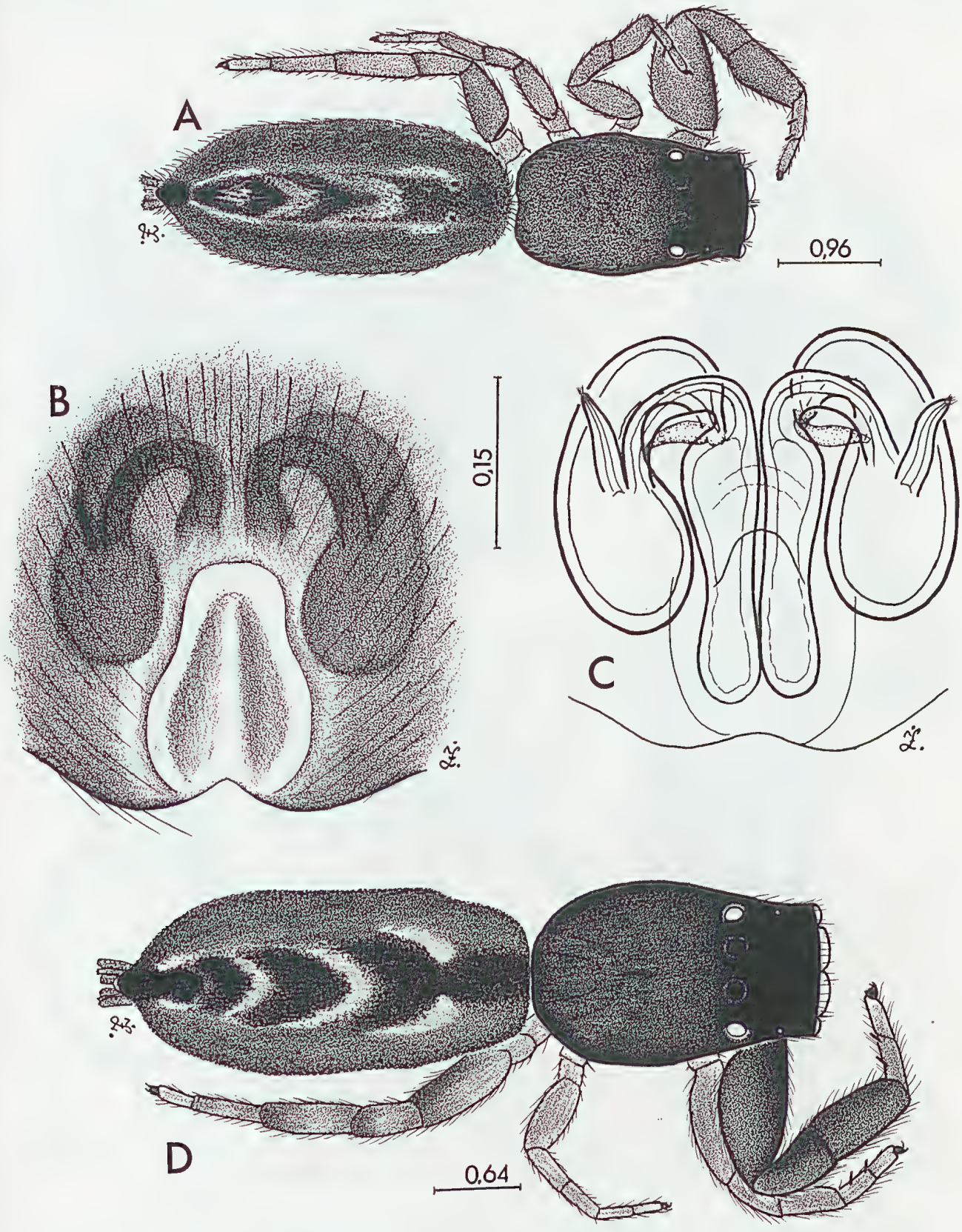



**Fig.32.** *Holoplatys fusca*, female (A-C Roachdale Nature Reserve, D Kangaroo Island).

dirty-brown. Venter with light median belt, darker laterally. Legs I brown, others lighter, all legs darker laterally and around joints.

Palpal organ (Fig.31B,C) similar to other representatives of the group but lateral tibial apophysis more curved.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1 or p1-1.

*Dimensions.* CL 2.07-2.26 (2.15), CW 1.27-1.48 (1.36), CW/CL 0.61-0.65 (0.62), EFL 0.62-0.68 (0.65), EFL/CL 0.29-0.31 (0.30), AEW 0.93-1.02 (0.96), PEW 0.96-1.05 (1.00), AL 2.48-2.79 (2.58).

**Female** (Figs 32A,D, 33A, 34A). Dorsal aspect and clypeus similar to that in male, lateral hairs on

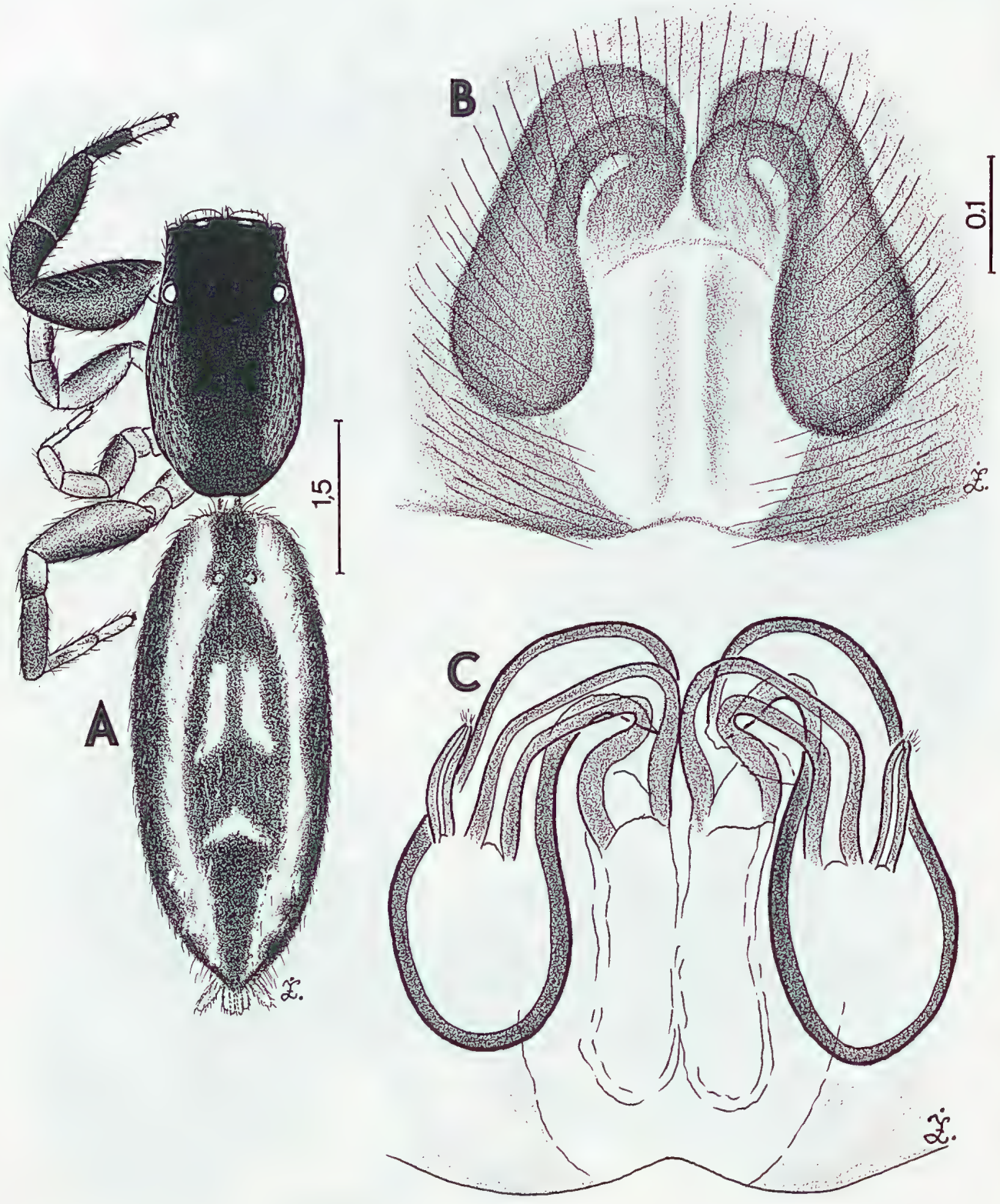



**Fig.33.** *Holoplatys fusca*, female from Geraldton area.

cephalothorax less numerous, abdomen without scutum. Chelicerae brown, pedipalps dirty-yellow, maxillae and labium dirty-brown, sternum orange with brown margin. Venter as in male. Legs coloured as in male, first ones relatively shorter.

Genitalia (Figs 32B,C, 33B,C, 34B,C) almost identical to other species of the group.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1 or p1-1.

*Dimensions.* CL 1.84-2.37 (2.15), CW 1.15-1.45 (1.30), CW/CL 0.59-0.61 (0.60), EFL 0.59-0.75 (0.65), EFL/CL 0.29-0.32 (0.30), AEW 0.89-1.05 (0.96), PEW 0.89-1.06 (0.98), AL 2.37-3.56 (3.00).

The female in the Berlin Collection (ZMB 1621) represents another genus, confirming doubts expressed by Karsch (1878).

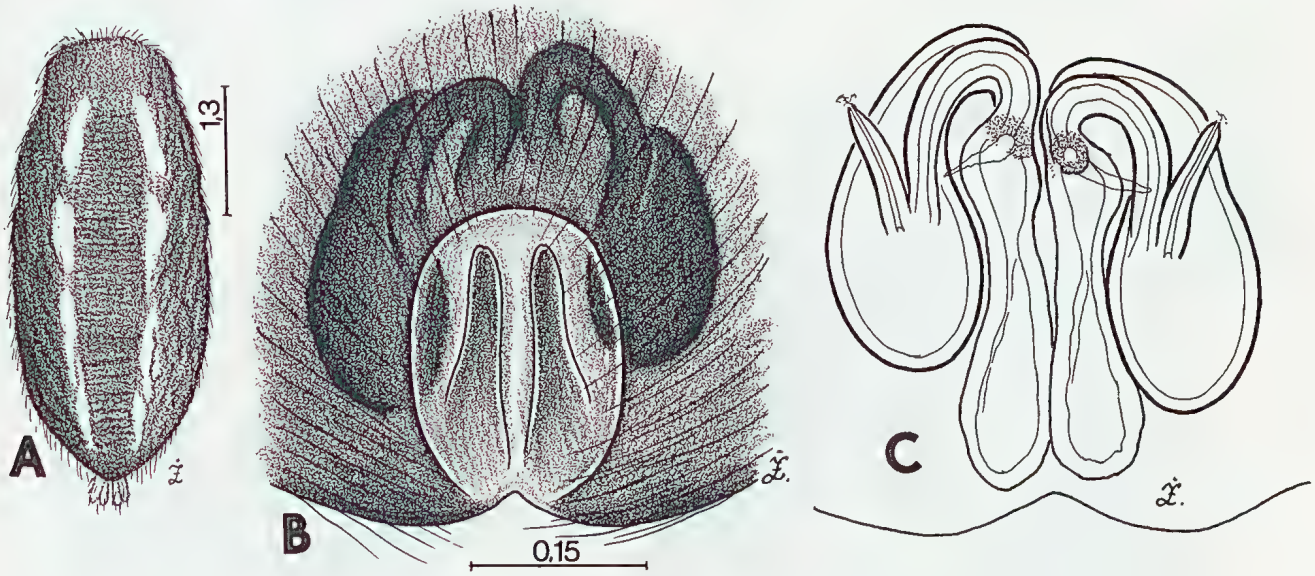
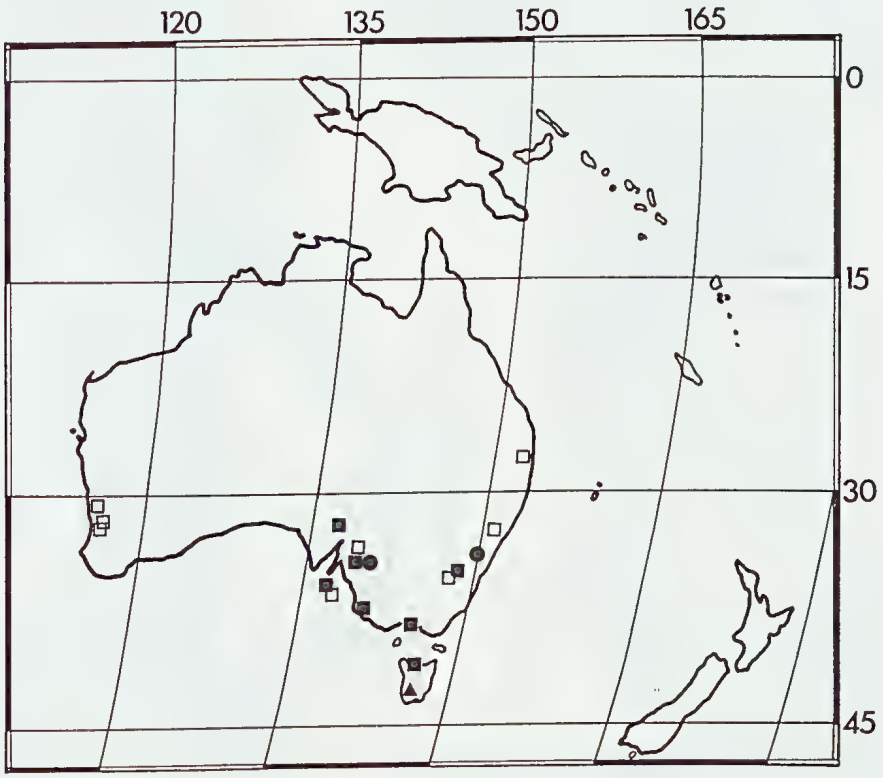



**Fig.34.** *Holoplatys fusca*, female from Mundaring Weir.




Map 5. Open square – *H. fusca* (Karsch); closed circle – *H. mascordi* n.sp.; closed square – *H. strzeleckii* n.sp.; closed triangle – *H. tasmanensis* n.sp.

### *Holoplatys pemberton* n.sp.

Figs 35-36, Map 4

**Material examined.** Western Australia: HOLOTYPE, male, Pemberton, under Karri bark, 20 Jan. 1943, WAMP 88/31; ALLOTYPE, female, Tenindewa, July 1926, 'Senex', WAMP 26/336.

**Diagnosis.** Cephalothorax without white lateral hairs, abdomen with herring-bone pattern, anterior scutum slightly visible. Clypeus fringed, with short, white hairs. Posterior edge of epigyne indented, central depression rather small, spermathecae and insemination ducts long.

**Male** (Fig.35A). Eye field brown with 2 darker central patches, thorax generally orange, dirty medially and marginally. Abdomen macerated, with traces of central herring-bone pattern and slightly visible anterior scutum. Spinnerets yellowish. Clypeus dirty-orange with fringe

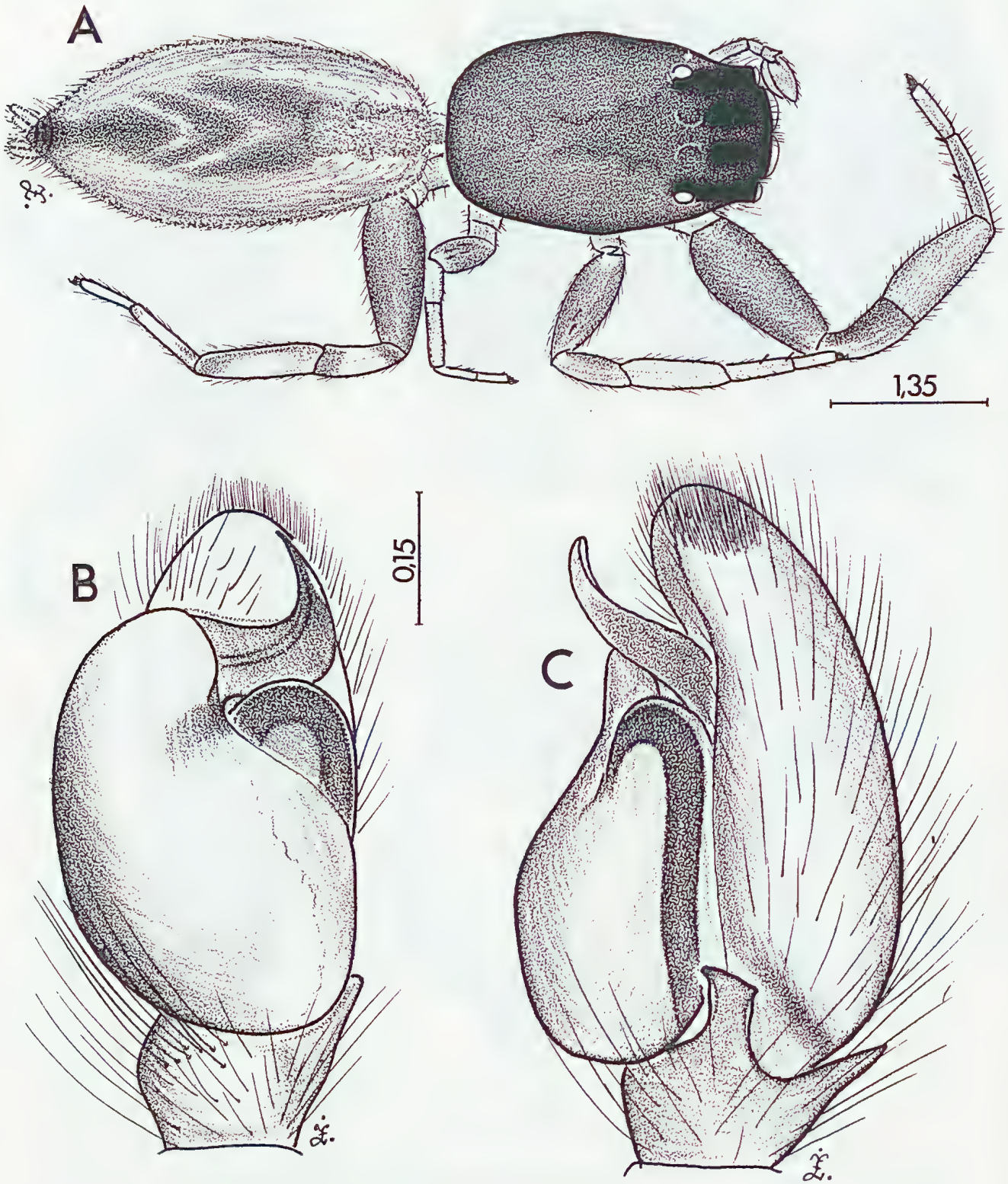



**Fig.35.** *Holoplatys pemberton*, male (holotype).

of whitish short hairs. Chelicerae and sternum dirty-orange, maxillae and labium orange. Venter light-grey. Legs orange, lighter distally, dirty laterally and around joints.

Palpal organ (Fig.35B,C) typical for the group. Tegulum without distinct depression, lateral tibial apophysis hooked.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.77, CW 1.72, CW/CL 0.62, EFL 0.79, EFL/CL 0.28, AEW 1.15, PEW 1.18, AL 3.56.

**Female** (Fig.36A). Colour pattern similar to the male.

Epigyne (Fig.36B,C) indented posteriorly, central depression smaller than in other species. Insemination ducts and spermathecae relatively long.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.22, CW 1.45, CW/CL 0.59, EFL 0.72, EFL/CL 0.29, AEW 1.05, PEW 1.09, AL 3.03.

### *Holoplatys mascordi* n.sp.

Fig.37, Map 5

**Material examined.** New South Wales: HOLOTYPE, male, Rivatts Creek, 8 Dec. 1966, R. Mascord, AMS KS18813;

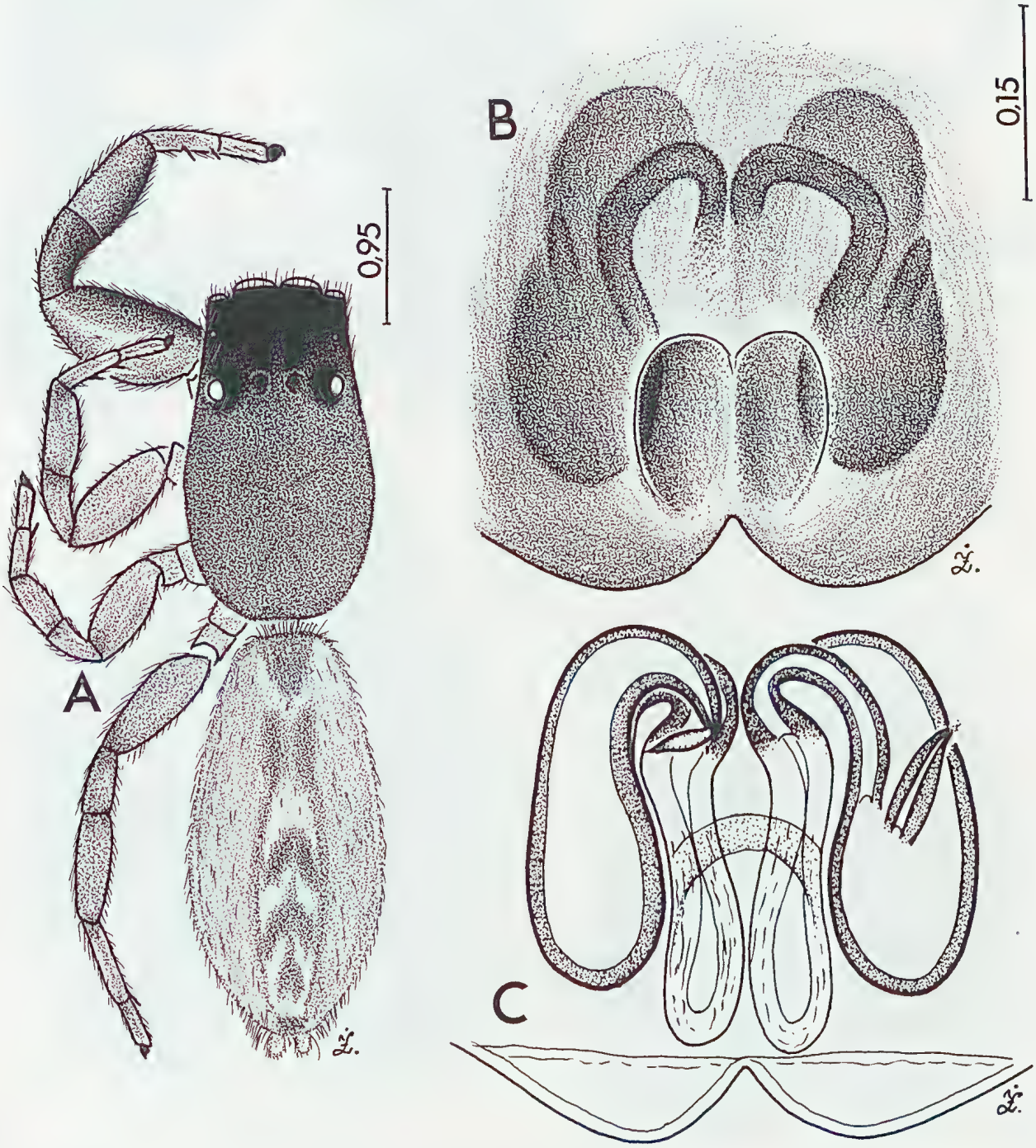



**Fig.36.** *Holoplatys pemberton*, female (allotype).

ALLOTYPE, female, same data, AMS KS19142; PARATYPES, male, female, same data, AMS KS1914, KS18814. South Australia: PARATYPE, male, 5 km south of Mylor, A.D. Austin, QMB S3592.

**Etymology.** The specific name is proposed in honour of Ramon Mascord, Australian naturalist and arachnologist.

**Diagnosis.** Embolus of palpal organ slightly longer and insemination ducts much longer than in other species of the group. Spermathecae and their accessory glands small.

**Male** (Fig.37A). Eye field brown with darker surroundings of eyes and 2 dark central spots. Thorax light-brown to brown with marginal white hairs. Abdomen

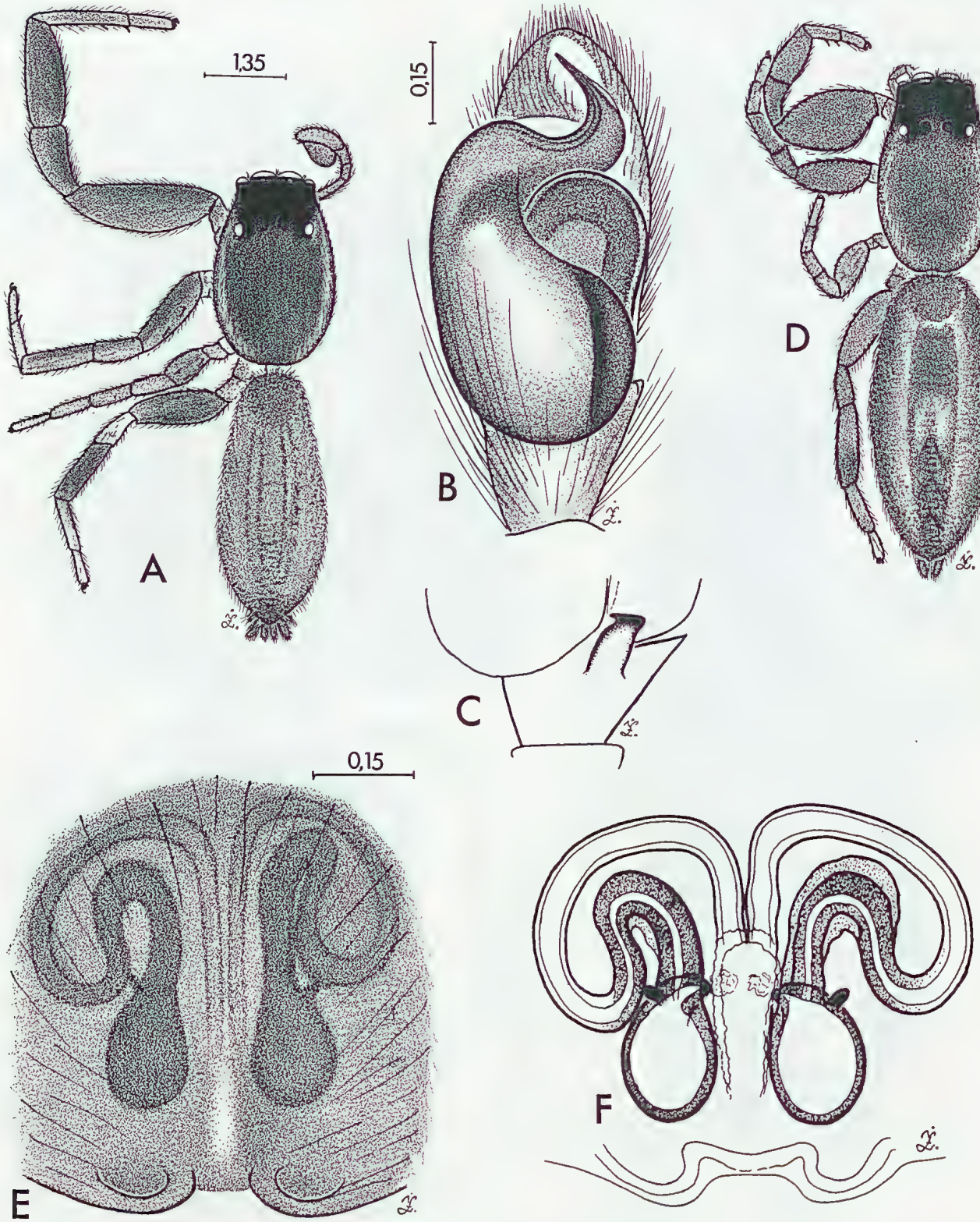



**Fig.37.** *Holoplatys mascordi*, A-C male (holotype), D-F female (allotype).

beige to grey with darker pattern along its central part. Anterior scutum slightly visible. Spinnerets grey. Clypeus brown with single grey hairs. Chelicerae brown, maxillae and labium honey-yellow, sternum orange with darker margin, venter beige. Legs I orange-brown to brown, long. Other legs generally lighter, darker laterally.

Palpal organ (Fig.37B,C) similar to other species of the group but embolus longer.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.95-3.23 (3.11), CW 1.81-2.11 (1.98), CW/CL 0.61-0.66 (0.63), EFL 0.82-0.92 (0.87), EFL/CL 0.27-0.29 (0.28), AEW 1.19-1.32 (1.27), PEW 1.22-1.38 (1.30), AL 3.82-4.09 (3.91).

**Female** (Fig.37D). Colour pattern generally similar to the male. Abdomen with traces of herring-bone pattern and slightly visible anterior scutum. Spinnerets dark-grey. Clypeus blackish with single grey hairs. Chelicerae dark-brown, pedipalps lighter. Maxillae and labium brown, sternum lighter with darker margin. Venter grey. Legs I orange to brown, distally and dorsoventrally lighter, other legs lighter.

Genitalia (Fig.37E-F) with very long insemination ducts, their distal parts more sclerotised. Spermathecae and accessory glands small.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 2.57-3.03 (2.80), CW 1.65-1.95 (1.80), CW/CL 0.64, EFL 0.72-0.79 (0.75), EFL/CL 0.26-0.28 (0.27), AEW 1.06-1.18 (1.12), PEW 1.06-1.18 (1.12), AL 3.56-4.62 (4.11).

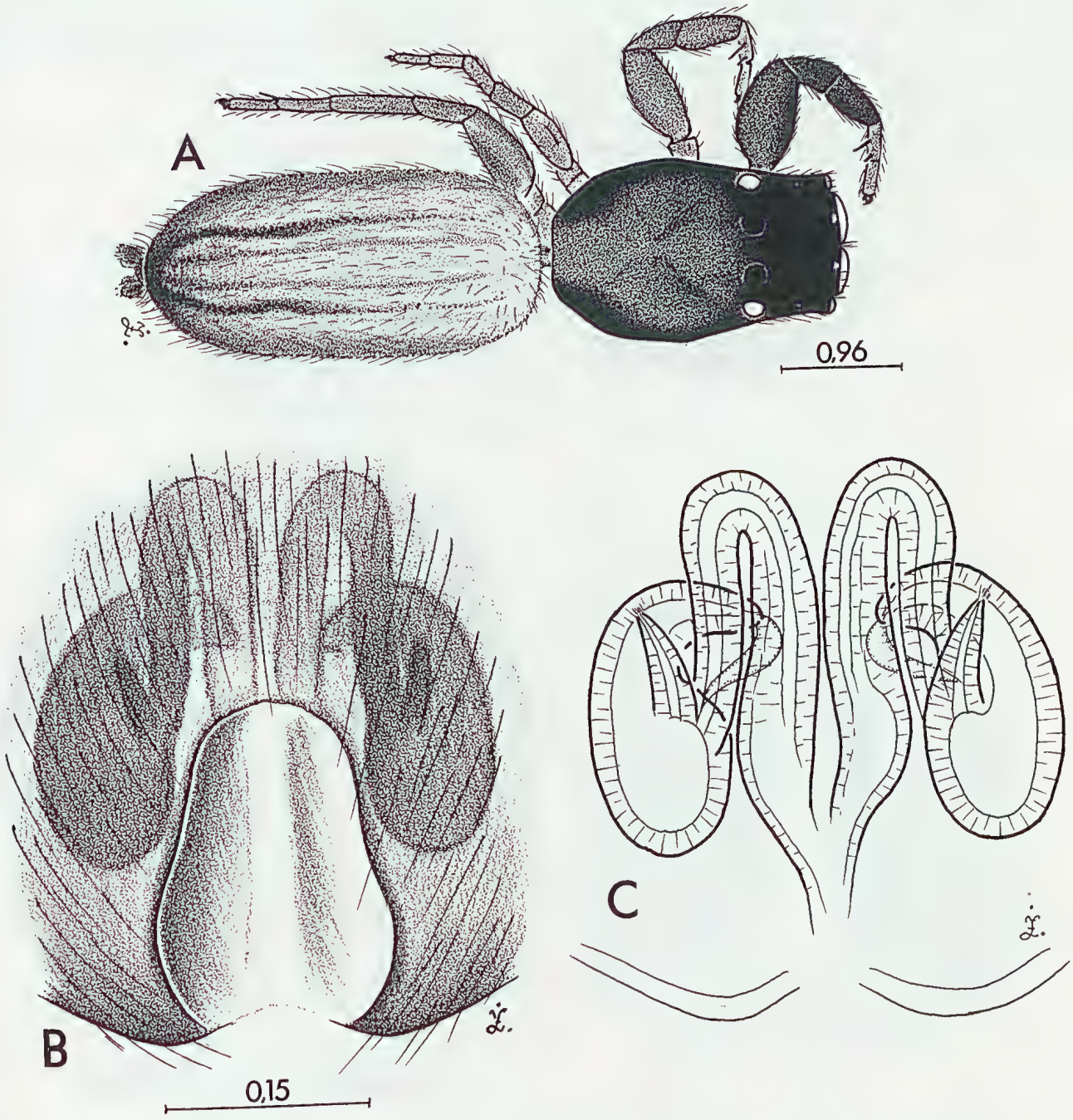



**Fig.38.** *Holoplatys braemarensis*, female (holotype).

### *Holoplatys braemarensis* n.sp.

Fig.38, Map 4

**Material examined.** Queensland: HOLOTYPE, female, PARATYPE, female, Braemar State Forest, litter, 4-8 Feb. 1980, R. Raven, QMB S3584.

**Diagnosis.** Cephalothorax coriaceous on eye field, its sides much darker than dorsal part. Proximal spines on metatarsus I and II twice as long as distal ones.

**Male.** The male is unknown.

**Female** (Fig.38A). Eye field coriaceous dark-brown, lateral surfaces of cephalothorax of the same colour, median part of thorax orange-brown. Abdomen light-grey, darker posteriorly with longitudinal darker stripes. Spinnerets dark-grey. Clypeus dark-brown with single blackish and whitish hairs. Maxillae and labium dark-brown, the first with light tips, sternum dark-orange with brown margin, venter grey. Legs I dark-brown proximally, metatarsus and tarsus lighter. Other legs lighter.

Genitalia (Fig.38B,C). Insemination ducts longer than in other species of the group.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r1-0.

*Dimensions.* CL 2.57-2.59 (2.58), CW 1.58-1.65 (1.61), CW/CL 0.61-0.63 (0.62), EFL 0.74, EFL/CL 0.28, AEW 1.20-1.22 (1.21), PEW 1.28-1.32 (1.30), AL 2.97-3.56 (3.26).

### *Holoplatys julimarina* n.sp.

Fig.39, Map 4

**Material examined.** Western Australia: HOLOTYPE, female, PARATYPE, juvenile, Julimar State Forest, north-east Perth, under *Eucalyptus* bark, 19 Sept. 1988, M. Zabka, WAMP 88/2382-3.

**Diagnosis.** Insemination ducts very long, forming

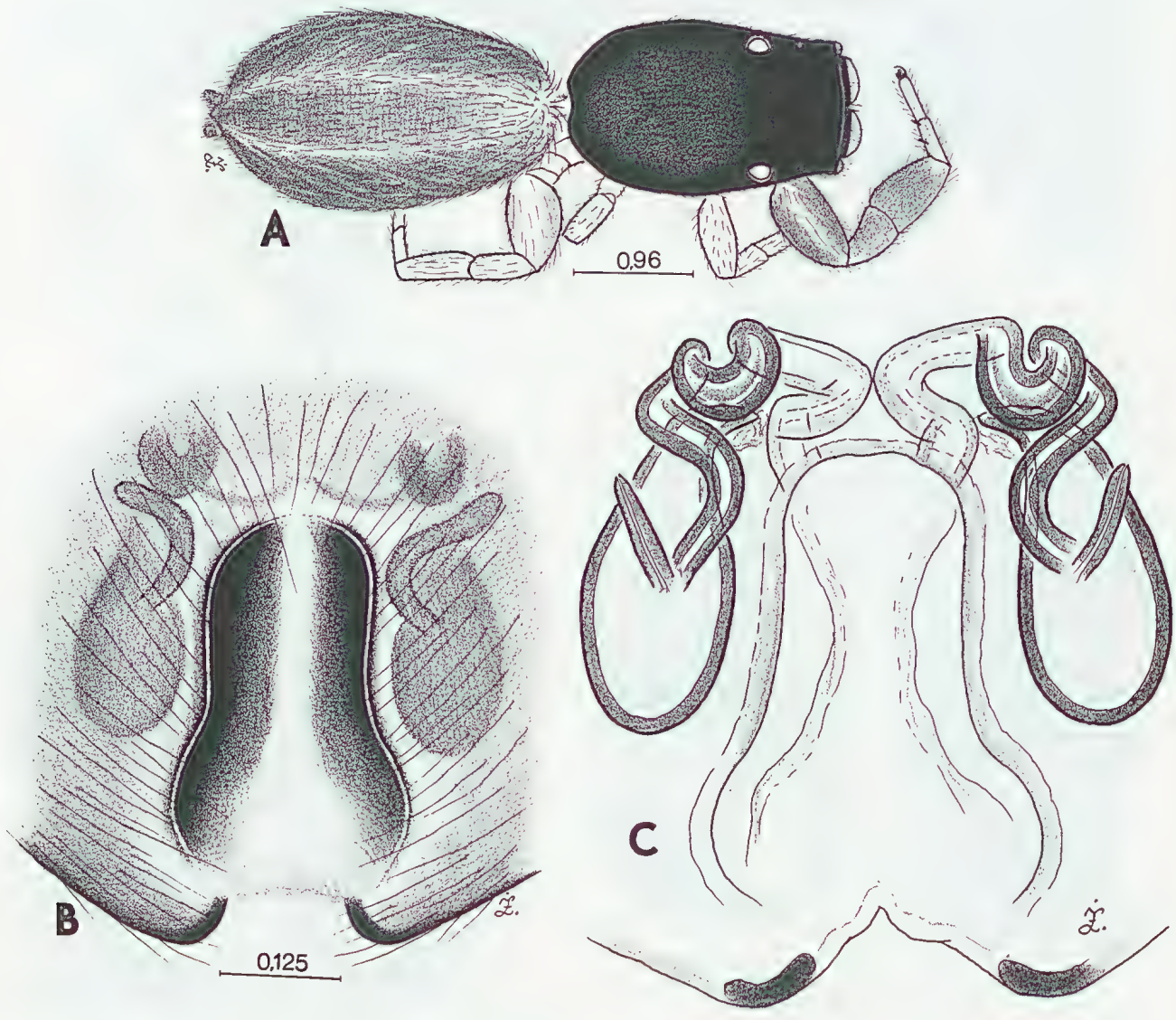



**Fig.39.** *Holoplatys julimarina*, female (holotype).

several loops.

**Male.** The male is unknown.

**Female** (Fig.39A). Eye field black, thorax slightly lighter, abdomen macerated, dark-grey, probably lighter medially, spinnerets dark-grey. Clypeus black, chelicerae dark-brown, pedipalps honey-yellow, maxillae and labium dark-brown with lighter tips. Sternum dirty-orange, venter beige. Legs I orange-brown, others successively lighter.

Epigyne (Fig.39B,C) with large central depression, insemination ducts very long, forming several loops.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.35, CW 1.43, CW/CL 0.60, EFL 0.75, EFL/CL 0.31, AEW 1.10, PEW 1.15, AL 2.85.

## The *grassalis* Group

The group consists of eight species (one of them described as incertae sedis), spread from subtropical Queensland, through New South Wales, South Australia and Western Australia. Body size tiny to medium (2.23-4.89), some of them with transverse spots of white hairs on abdomen surface. Tegulum of palpal organ oval, dorsal apophysis on tibia present. Species included: *grassalis, chudalupensis, desertina, daviesae, dejongi, kalgoorlie, embolica, lhotskyi.*

### *Holoplatys grassalis* n.sp.

Fig.40, Map 6

**Material examined.** Western Australia: HOLOTYPE, male, Grass Patch, house verandah, 29 Sept. 1983, A.F. Longbottom, WAMP 88/6.

**Diagnosis.** Relatively large, abdomen rather short, clypeus and chelicerae with clusters of light hairs. Tibial apophyses of palpal organ relatively small, pointed.

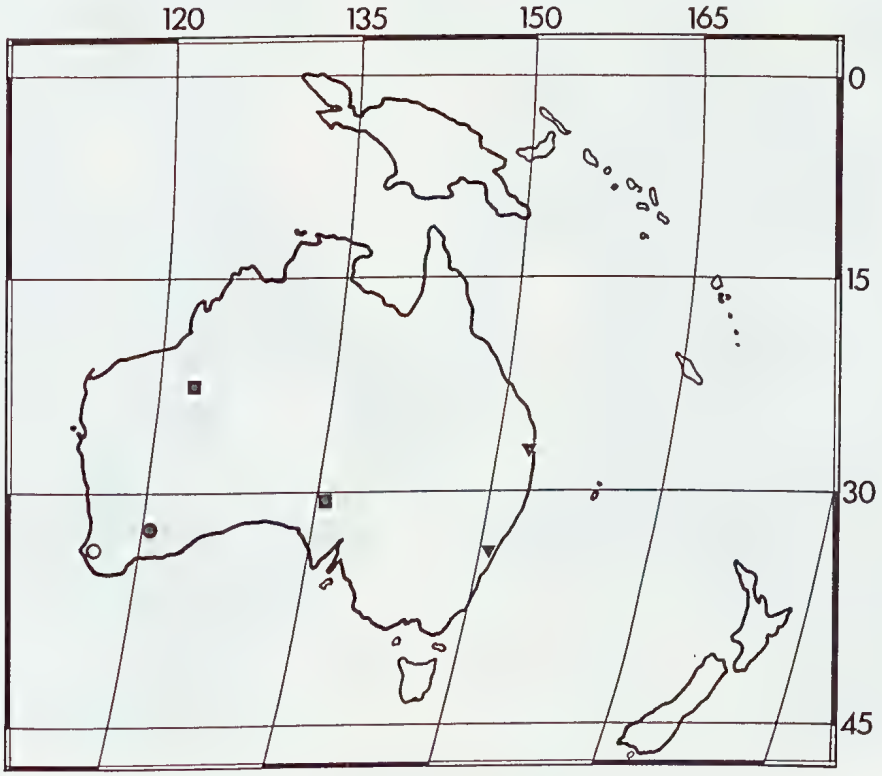
**Male** (Fig.40A). Eye field black. Thorax brown, lighter around fovea, darker marginally. Abdomen with indistinct dirty-orange anterior scutum and herring-bone median pattern. Spinnerets black. Clypeus brown-black with short scale-like hairs in the middle and with fringe of silver hairs. Chelicerae dirty-brown with tufts of silver hairs. Maxillae and labium greyish-brown with lighter tips, sternum orange, marginally darker with white hairs. Venter grey centrally, darker laterally and posteriorly with longitudinal light stripes. Legs I long, dirty-brown, tarsus yellow, patella and tibia fringed. Other legs generally lighter, darker laterally and around joints.

Palpal organ (Fig.40B,C). Embolus shorter than in other representatives of the group.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.22, CW 1.62, CW/CL 0.72, EFL 0.76, EFL/CL 0.34, AEW 1.15, PEW 1.16, AL 2.67.

**Female.** The female is unknown.




Map 6. Open circle – *Holoplatys chudalupensis* n.sp.; closed inverted triangle – *H. daviesae* n.sp.; closed square – *H. desertina* n.sp.; closed circle – *H. grassalis* n.sp.

### *Holoplatys chudalupensis* n.sp.

Fig.41, Map 6

**Material examined.** Western Australia: HOLOTYPE, male, on top of Mount Chudalup, 3 Apr. 1988, J.M. Waldock, WAMP 88/21.

**Diagnosis.** Cephalothorax bicoloured, abdomen dark, clypeus fringed, distal segments of legs (except legs III) black.

**Male** (Fig.14A). Eye field black, thorax orange, darker around lower margins. Abdomen with anterior dirty-brown scutum and lateral fringes of white hairs, posteriorly almost black with light irregular pattern. Spinnerets black. Clypeus brown with fringe of white short hairs. Chelicerae dirty-

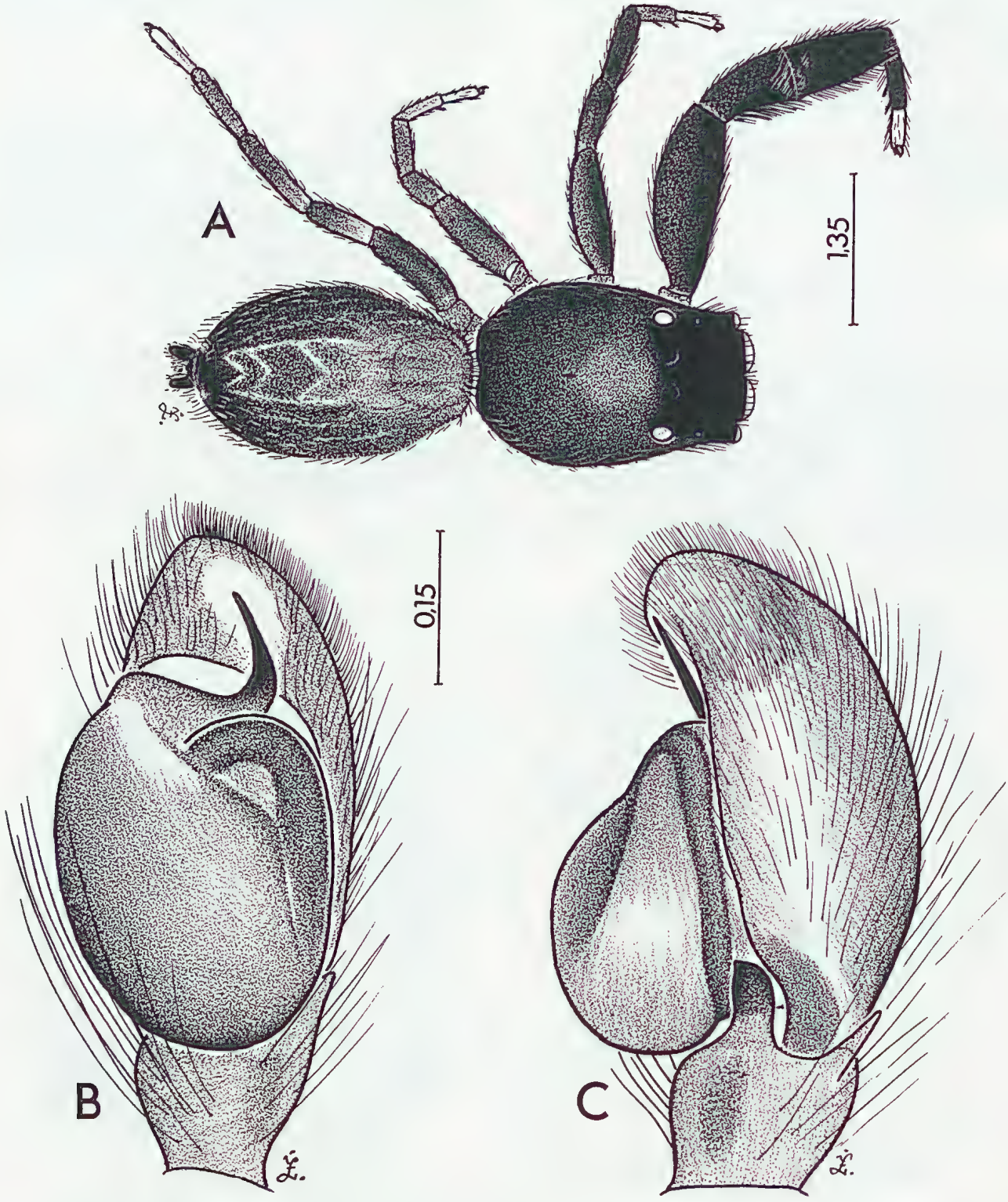



**Fig.40.** *Holoplatys grassalis*, male (holotype).

yellow, maxillae, labium and sternum yellow. Venter dirty-beige anteriorly, posteriorly and laterally darker. Coxa, trochanter and proximal femur of legs I yellow, other segments black. Patellae, tibiae and metatarsi II and IV black, other segments yellow. Legs III yellow.

Palpal organ (Fig.41B,C). Embolus long, wavy distally, tegulum relatively small.

*Leg spination.* mI: p1-1, r1-1.

*Dimensions.* CL 1.40, CW 0.90, CW/CL 0.64, EFL 0.45, EFL/CL 0.32, AEW 0.77, PEW 0.77, AL 1.25.

**Female.** The female is unknown.

***Holoplatys desertina* n.sp.**

Fig.42, Map 6

**Material examined.** South Australia: HOLOTYPE, female, 175 km west Vokes Hill Corner, Great Victoria Desert, under bark of *Eucalyptus concinna*, 29 Aug. 1980, G.J. Baker, SAMA N1988337. Western Australia: PARATYPE, female, Rudall River camp, river gums, 17 July 1988, A.E. de Jong, Wamp 89/285.

**Diagnosis.** Abdomen wider than in other species. Insemination ducts meandering.

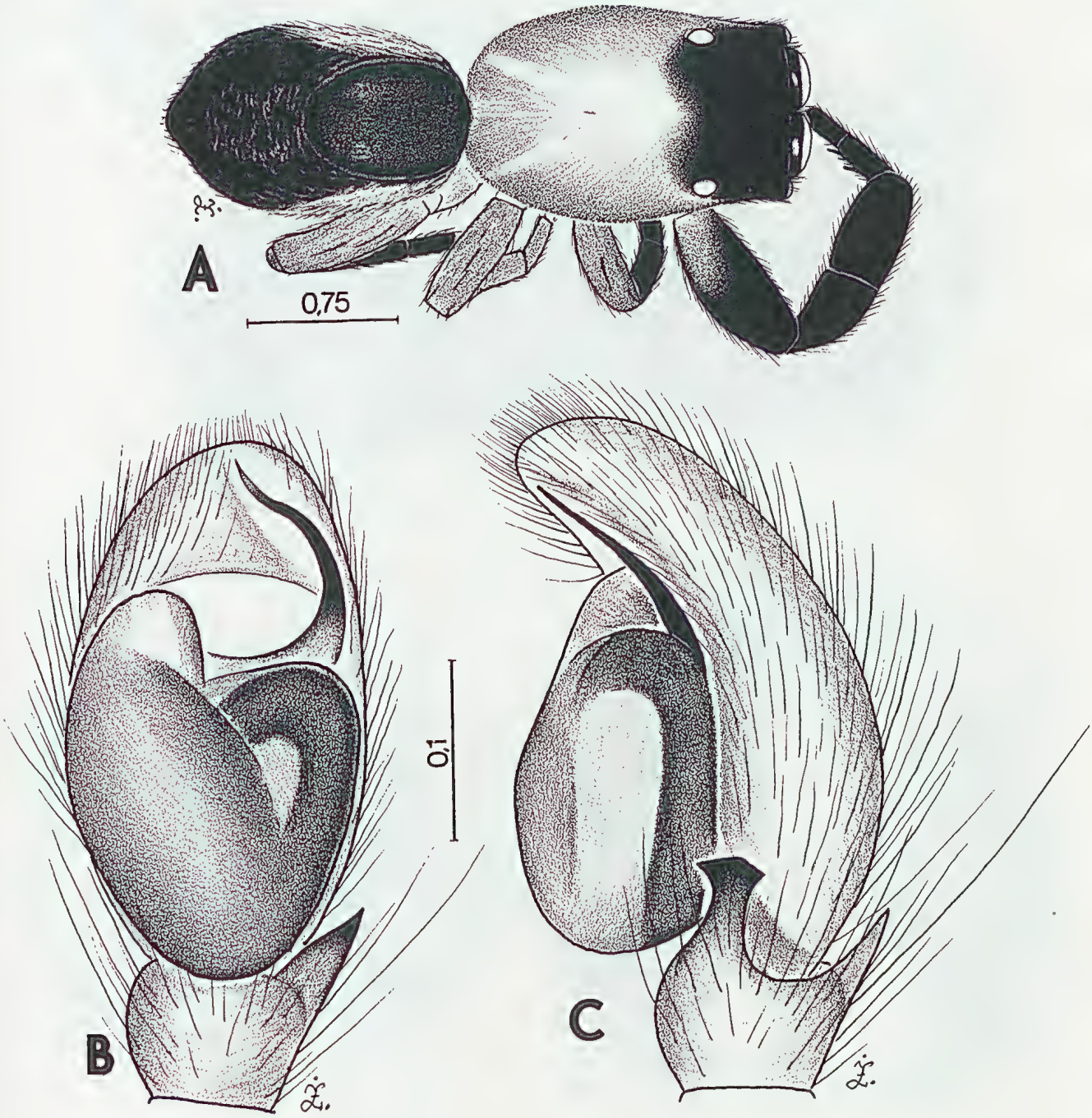



**Fig.41.** *Holoplatys chudalupensis*, male (holotype).

**Male.** The male is unknown.

**Female** (Fig.42A). Eye field black, thorax brown, dirty marginally. Abdomen grey-brown, lighter medially and anteriorly with pale transverse stripes. Spinnerets grey-brown. Clypeus black-brown, chelicerae, maxillae, labium and sternum dirty-orange. Venter beige centrally, dark-grey laterally. Legs yellow-orange.

Genitalia (Fig.42B,C) with long, meandering insemination ducts, accessory glands long and thin.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 1.45, CW 0.86, CW/CL 0.59, EFL 0.49, EFL/CL 0.34, AEW 0.71, PEW 0.74, AL 2.04.

***Holoplatys daviesae* n.sp.**

Fig.43, Map 6

**Material examined.** Queensland: HOLOTYPE, male, Brisbane, dry *Eucalyptus* forest, under bark, Aug.-Sept. 1987, M. Zabka, AMS KS20586; ALLOTYPE, female, same data, KS20587; PARATYPE, male, same data, KS20584. New South Wales: PARATYPES, male, female, Bargo, on tree trunk, 24 Oct. 1987, M. Zabka, AMS KS20585.

**Etymology.** The specific name is proposed in honour of Dr Valerie Todd Davies, Australian arachnologist, honorary associate at Queensland Museum, Brisbane.

**Diagnosis.** Similar to *dejongi* but palpal organ more

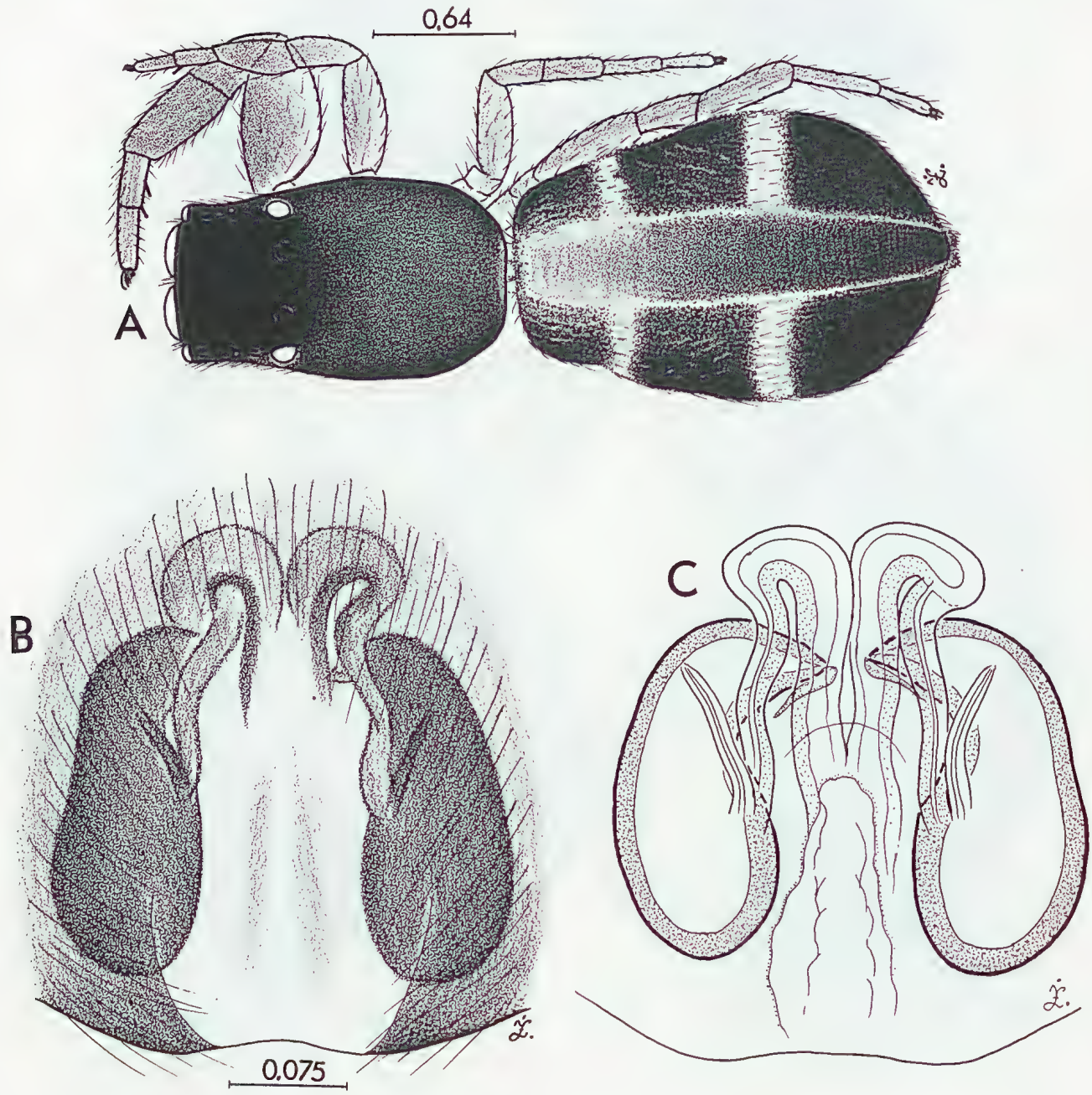



**Fig.42.** *Holoplatys desertina*, female (holotype).

delicate, tegulum smaller and embolus shorter.

**Male** (Fig.43A). Cephalothorax rather wide, generally dark, slightly lighter on eye field, with scattered white hairs. Abdomen dark-grey, Clypeus and chelicerae dark-brown. Maxillae, labium and sternum lighter, venter light to grey. Legs I brown, laterally darker, distally lighter, tarsi and metatarsi yellow. Other legs generally lighter.

Palpal organ (Fig.43B,C). Tegulum smaller than in the related *dejongi*, also lateral tibial apophysis and embolus of different shape.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 1.40-1.95 (1.62), CW 0.95-1.33 (1.07), CW/CL 0.62-0.67 (0.65), EFL 0.46-0.65 (0.53), EFL/CL 0.31-0.33 (0.32), AEW 0.62-0.85 (0.73), PEW 0.66-0.85 (0.75), AL 1.75-2.55 (2.15).

**Female.** Body form and colour pattern similar to the male, only abdominal scutum absent and legs lighter.

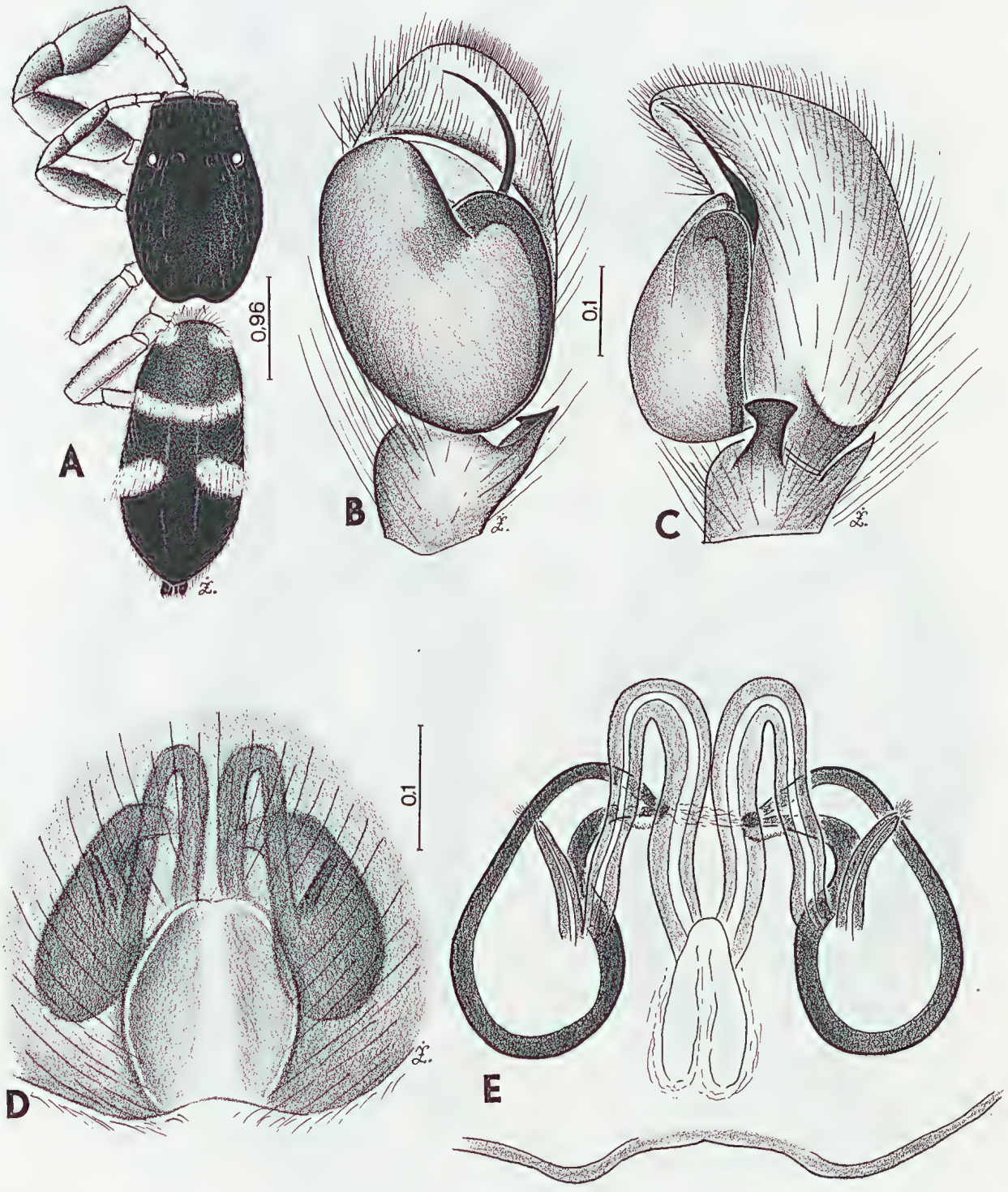



**Fig.43.** *Holoplatys daviesae*, A-C male (holotype), D,E female (allotype).

Genitalia (Fig.43D-E) with long insemination ducts, accessory glands long, curved laterally.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 1.56-1.75 (1.65), CW 0.92-1.15 (1.04), CW/CL 0.59-0.65 (0.62), EFL 0.47-0.55 (0.51), EFL/CL 0.30-0.31 (0.31), AEW 0.80, PEW 0.84, AL 2.20.

***Holoplatys dejongi* n.sp.**

Fig.44, Map 7

**Material examined.** Western Australia: HOLOTYPE, male, Parmelia, near Kwinana, 2 Oct. 1987, A.E. de Jong,

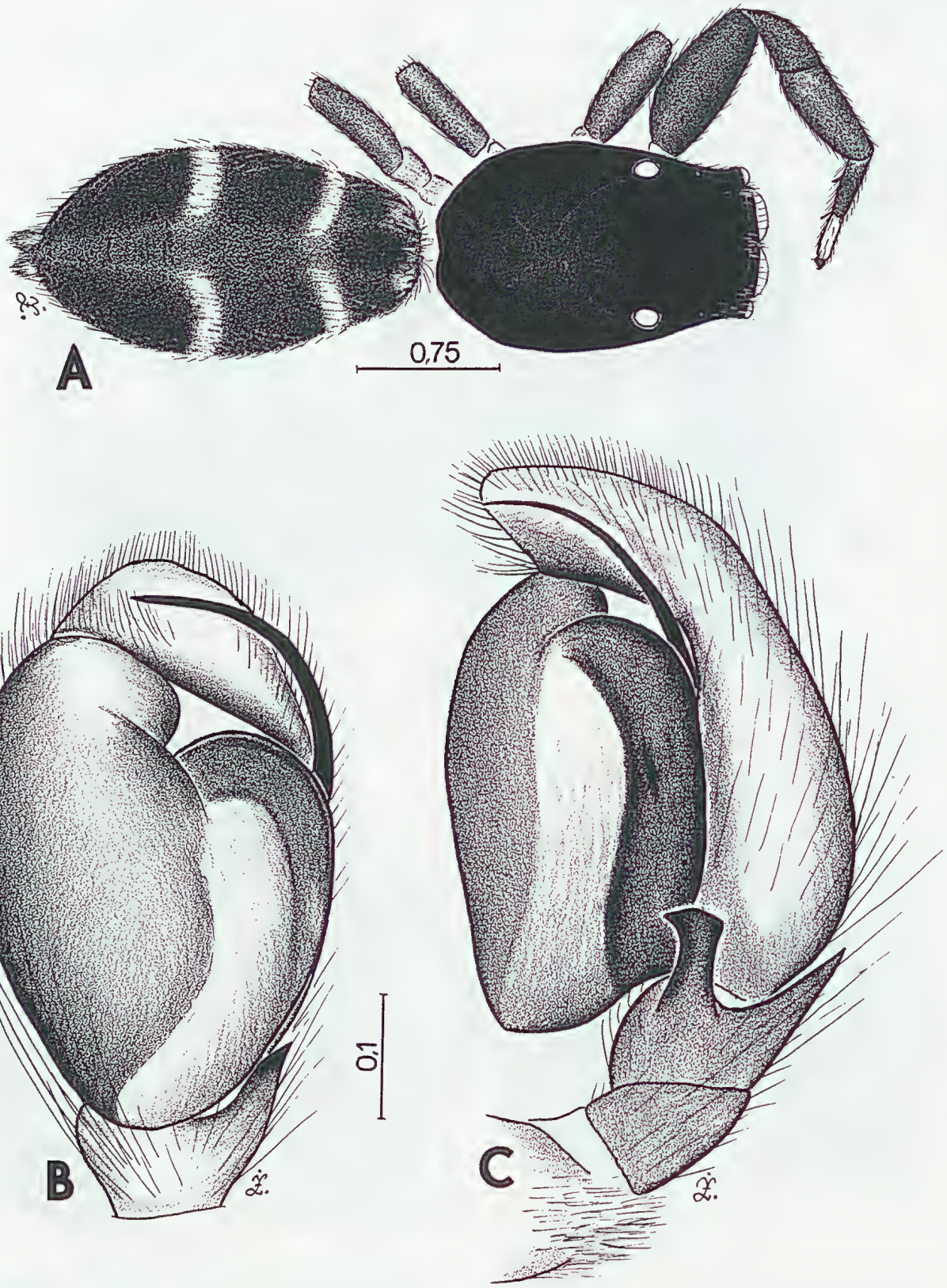



**Fig.44.** *Holoplatys dejongi*, male (holotype).

WAMP, 88/2155; PARATYPES, 2 males, 5 km west Lake Indoon, under *Eucalyptus* bark, 20 Sept. 1988, D. Knowles, M. Zabka, WAMP 88/2386-7.

**Etymology.** The specific name is proposed in honour of Mr Aris E. de Jong, naturalist from Western Australia, collector of many specimens described in this paper.

**Diagnosis.** Similar to *daviesae* but tegulum larger, embolus thicker and longer.

**Male** (Fig, 44A). Cephalothorax almost black. Abdomen dark-grey with broken transverse stripes of white hairs. Spinnerets dark. Clypeus dark, chelicerae dirty-grey, maxillae and labium slightly lighter, sternum dirty-brown, venter light centrally, laterally darker. Legs I grey-brown only tarsi lighter, also other legs generally lighter, especially their dorsoventral parts.

Palpal organ (Fig.44B,C) with massive tegulum, long embolus and femoral distal brush of white hairs.

*Leg spination.* mI: p1-1, r1-1.

*Dimensions.* CL 1.25-1.45 (1.35), CW 0.85-0.95 (0.89), CW/CL 0.65-0.68 (0.66), EFL 0.41-0.41 (0.43), EFL/CL 0.31-0.33 (0.32), AEW 0.62-0.70 (0.66), PEW 0.67-0.75 (0.70), AL 1.60-1.85 (1.68).

**Female.** The female is unknown.

***Holoplatys kalgoorlie* n.sp.**

Fig.45, Map 7

**Material examined.** Western Australia: HOLOTYPE, male, PARATYPE, juvenile, Kalgoorlie, Mar. 1968, WAMP 88/15-16.

**Diagnosis.** Small spider (male less than 3.5 mm), colour pattern generally lighter than in other representatives of the group, lateral tibial apophysis of different shape.

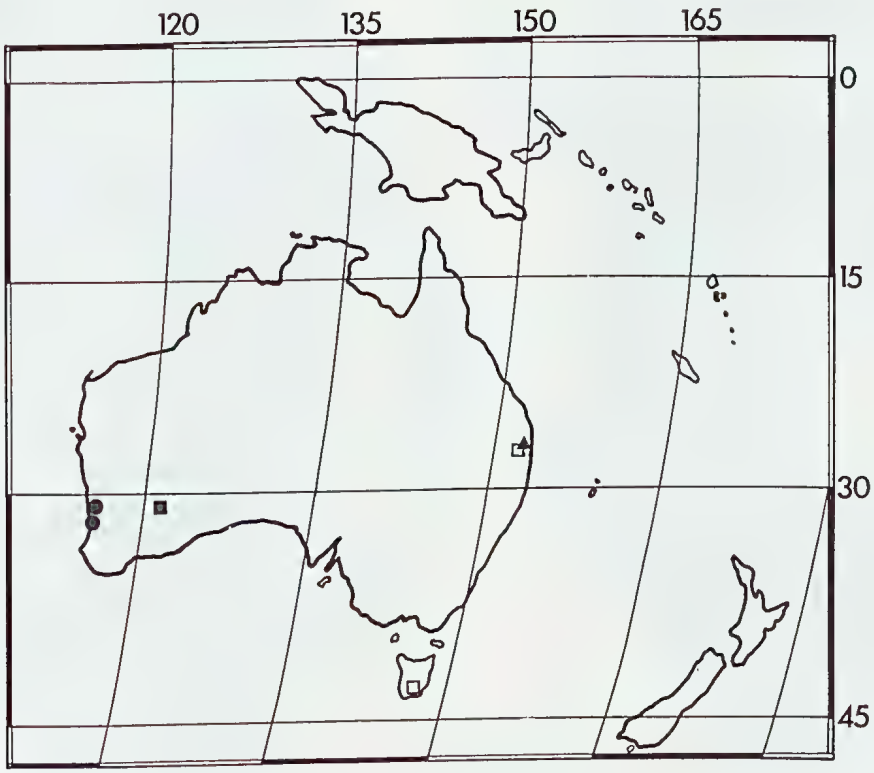
**Male** (Fig.45A). Eye field dark with 2 black spots, thorax pale-brown with dirty-brown margin. Anterior part of abdomen more sclerotised with light and grey pattern. Spinnerets yellowish. Clypeus blackish with single dark-grey hairs. Chelicerae dirty-brown, pedipalps pale-orange. Maxillae, labium and sternum honey-yellow, sternum lighter with darker margin, venter beige. Legs I dirty-orange-brown, darker prolaterally and around joints, legs II and III dirty-yellow.

Palpal organ as illustrated in Figure 45B,C.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 1.48, CW 1.02, CW/CL 0.68, EFL 0.53, EFL/CL 0.36, AEW 0.72, PEW 0.76, AL 1.92.

**Female.** The female is unknown.




Map 7. Closed circle – *Holoplatys dejongi* n.sp.; closed triangle – *H. embolica* n.sp.; closed square – *H. kalgoorlie* n.sp.; open square – *H. lhotskyi* n.sp.

### *Holoplatys embolica* n.sp.

Fig.46, Map 7

**Material examined.** Queensland: HOLOTYPE, male, Brisbane, Rochedale S.F., under bark, 7 Oct. 1980, V. Davies, R. Raven, QMB S3553.

**Diagnosis.** Tiny spider, tegulum as wide as long, embolus long, thick and curved, tibial apophysis cone-shaped more like *planissima* group.

**Male** (Fig.46A). Eye field almost black, thorax dirty-honey, darker centrally and marginally. Abdomen damaged with anterior scutum and black and orange

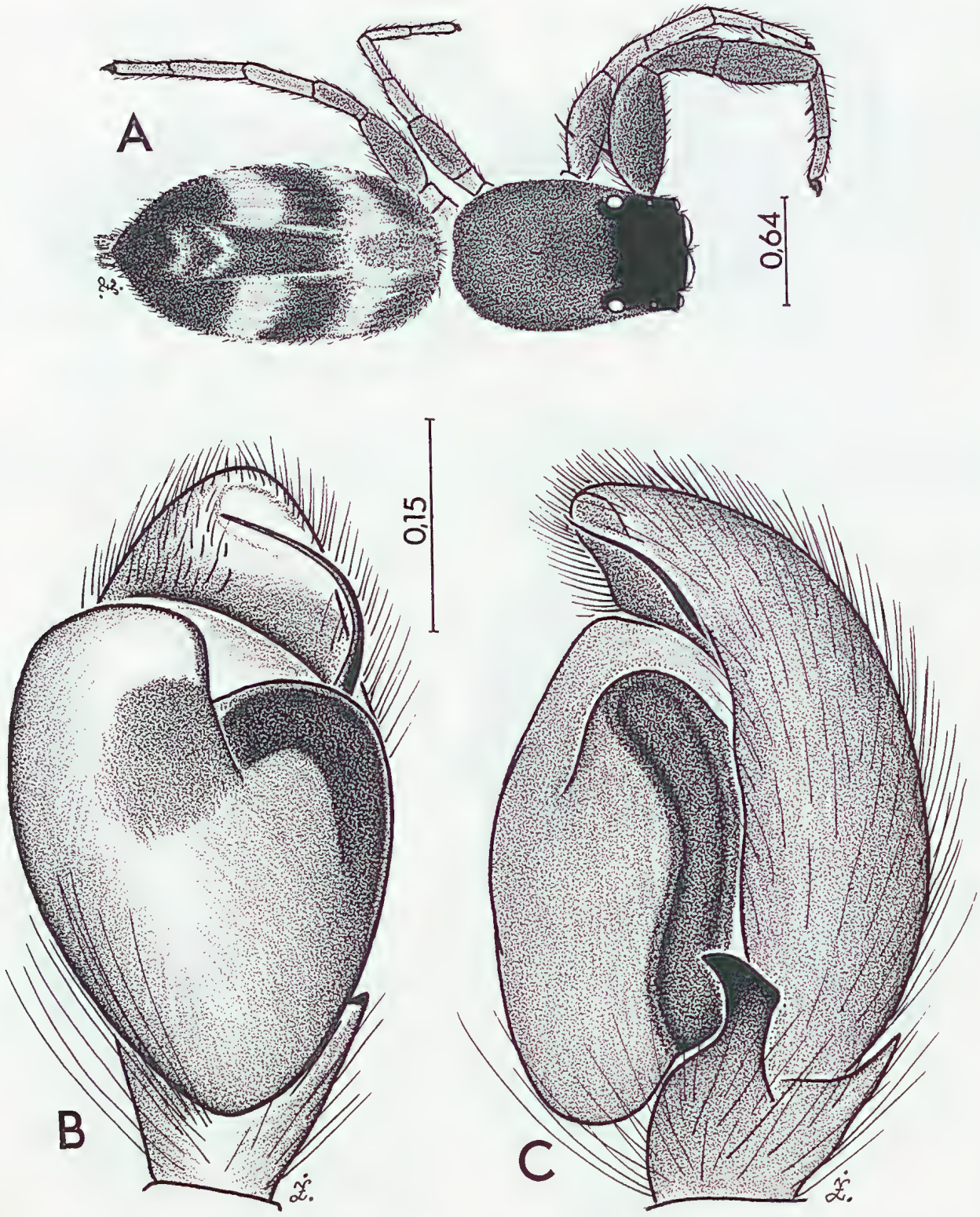



**Fig.45.** *Holoplatys kalgoorlie*, male (holotype).

pattern. Clypeus almost black with single light hairs. Chelicerae, pedipalps, maxillae and labium orange, sternum anteriorly orange, posterially dirty. Venter centrally beige, laterally darker. Legs I with dirty-orange lateral surface of femur. Patella, tibia, metatarsus and tarsus yellow. Other legs more delicate, slightly lighter.

Palpal organ as illustrated in Figure 46B,C.

*Leg spination.* mI: p0-1, r1-1.

*Dimensions.* CL 1.05, CW 0.66, CW/CL 0.62, EFL 0.36, EFL/CL 0.34, AEW 0.46, PEW 0.47, AL 1.18.

**Female.** The female is unknown.

***Holoplatys lhotskyi* n.sp.** (incertae sedis)

Figs 47-48, Map 7

**Material examined.** Queensland: HOLOTYPE, male, Brisbane, Fig Tree Pocket, 29 Jan. 1973, V. Davies, QMB

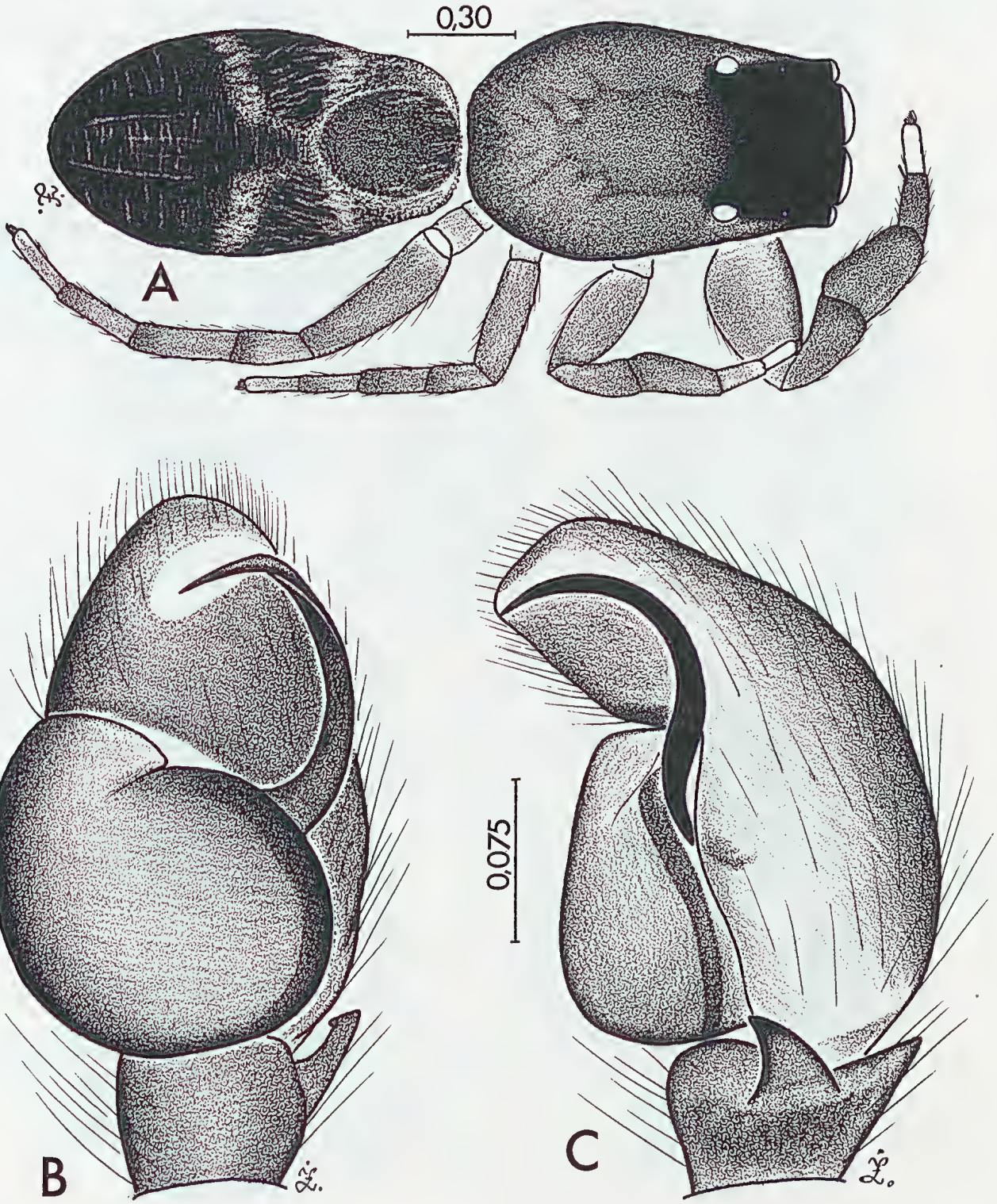



**Fig.46.** *Holoplatys embolica*, male (holotype).

S3568; ALLOTYPE, female, Rochedale S.F., beating, 31 Jan. 1980, V. Davies, R. Raven, QMB S3555; PARATYPES, 2 females, same data, 21 Apr. 1980, QMB S3583; female, same data, 1 July 1980, QMB S3556. Tasmania: male, *Holoplatys* sp. Spider Den (North Lune), 5 Feb. 1988, A. Clarke, AMS KS18882.

**Etymology.** The specific name is proposed in honour of John Lhotsky, Polish nineteenth-century

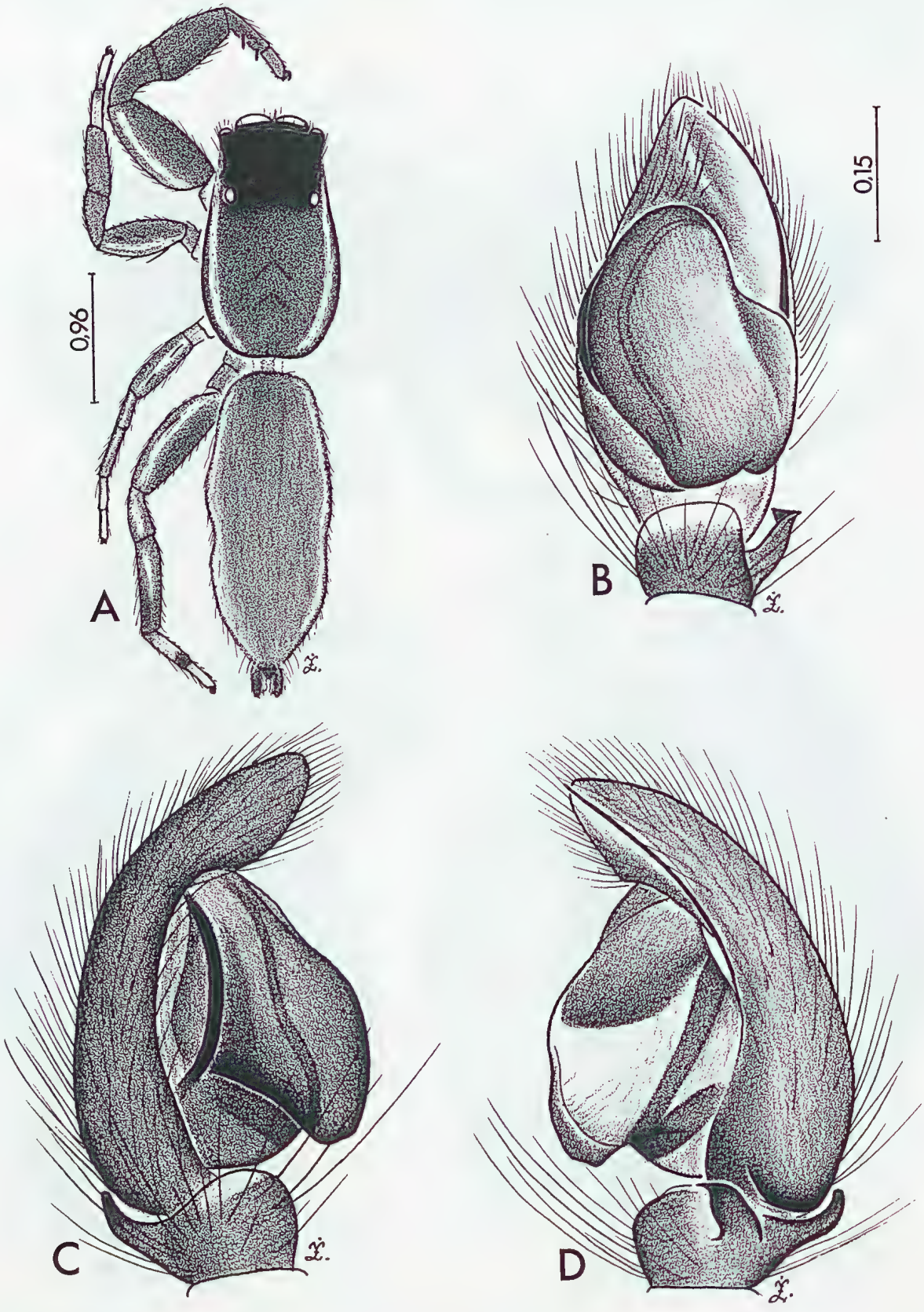



**Fig.47.** *Holoplatys lhotskyi*, male (holotype).

naturalist and explorer of the Australian Alps and Canberra area.

**Diagnosis.** Small, slender spider. Lateral stripes of white hairs along body. Palpal organ untypical for the genus: tegulum of irregular shape, embolus very long and thin, dorsal tibial apophysis large.

**Male** (Fig.47A). Eye field almost black, thorax dirty-brown with white lateral stripes. Abdomen yellow-orange with light band and dark lateral surfaces. Spinnerets dark-grey. Clypeus black with whitish hairs. Chelicerae, maxillae, labium and sternum dirty-orange-brown, venter dirty-beige. Legs I dirty-brown, lighter distally, darker around joints. Dorsal parts of basal segments with white stripe. Other legs lighter.

Palpal organ as illustrated in Figure 47B-D.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 1.75, CW 1.12, CW/CL 0.64, EFL 0.61, EFL/CL 0.34, AEW 0.79, PEW 0.76, AL 2.31.

**Female** (Fig.48A). Cephalothorax as in male. Abdomen beige, slightly darker centrally and

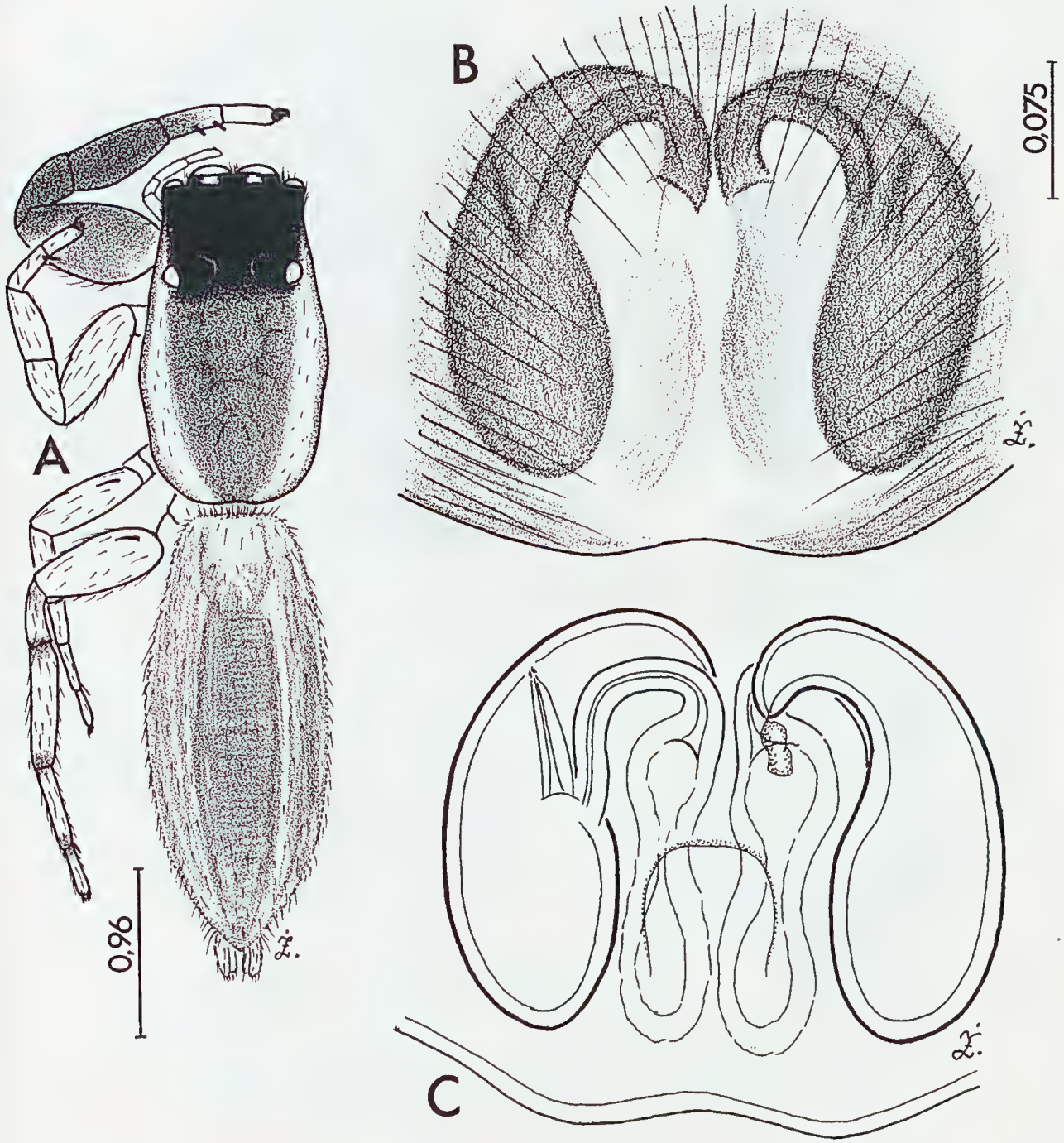



**Fig.48.** *Holoplatys lhotskyi*, female (allotype).

laterally, spinnerets beige. Clypeus brown with fringe of white hairs. Chelicerae, maxillae and labium dirty-brown. Pedipalps and sternum yellow, the last with brown margin; venter beige-grey. Distal femur, patella, tibia and proximal metatarsus of first legs dirty-brown, the rest and other legs yellow.

Genitalia (Fig.48B,C) similar to *planissima* group, with long spermathecae and insemination ducts.

*Leg spination.* mI: p1-1, r1-1; mII: p0-1.

*Dimensions.* CL 1.84-2.17 (2.03), CW 1.12-1.25 (1.21), CW/CL 0.56-0.62 (0.59), EFL 0.59-0.66 (0.62), EFL/CL 0.29-0.32 (0.30), AEW 0.86-0.96 (0.90), PEW 0.86-0.99 (0.93), AL 2.18-2.62 (2.45).

Tasmanian specimen identical in genitalic structure, but body colour almost black, which makes its status uncertain.

## The *panthera* Group

The group consists of three species known from scattered localities in Papua New Guinea, Queensland and South Australia. Body small (2.44-4.52), cephalothorax almost parallel-sided. Male palpal organ with lateral and dorsal apophyses on tibia. Genitalia structure suggests close relationship with *planissima* group. Species included: *panthera, minuta, queenslandica.*

### *Holoplatys panthera* n.sp.

Fig.49, Map 8

**Material examined.** South Australia: HOLOTYPE, female, Ooldea, A.M. Lea, SAMA N1988338.

**Etymology.** The specific name refers to panther-like spots on abdomen.

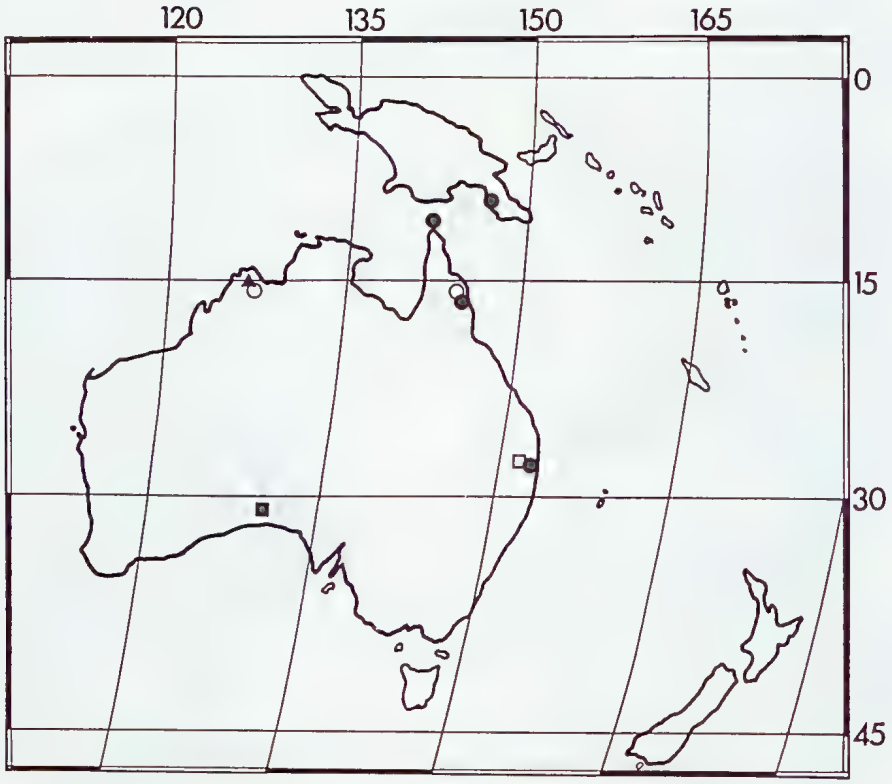
**Diagnosis.** Cephalothorax textured, abdomen spotted, metatarsal spines on legs I and II much longer than in other species of the genus.

**Male.** The male is unknown.

**Female** (Fig.49C). Cephalothorax slender, slightly higher than usually, strippled (textured). Single white hairs scattered around eyes. Abdomen light, darker posteriorly with dark panther-like spots. Spinnerets grey-brown. Clypeus brown with single light hairs. Chelicerae light-brown, pedipalps whitish-yellow. Maxillae and labium dirty-orange, sternum darker, venter with dark spots as on dorsal surface. Legs I with dark-brown patella, tibia and metatarsus, femur lighter, especially dorsoventrally, tarsus yellow. Other legs yellow, slightly darker around joints. Metatarsal spines on legs I and II long.

Genitalia (Fig.49A,B) similar to the *planissima* group.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1, r1-0.




Map 8. Closed triangle – *Holoplatys bicolor* Simon; open circle – *H. bicoloroides* n.sp.; open square – *H. minuta* n.sp.; closed square – *H. panthera* n.sp.; closed circle – *H. queenslandica* n.sp.

*Dimensions*. CL 1.70, CW 0.96, CW/CL 0.56, EFL 0.62. EFL/CL 0.36, AEW 0.85, PEW 0.85, AL 2.82.

### *Holoplatys minuta* n.sp.

Fig.50, Map 8

**Material examined.** Queensland: HOLOTYPE, female, Brisbane, Lake Broadwater, brigalow, melon hole area, 26 Jan. 1985, V. Davies, J. Gallon, QMB S3598.

**Diagnosis.** Insemination ducts long and broad, narrowing distally, metatarsal spines on legs II absent.

**Male.** The male is unknown.

**Female** (Fig.50A). Eye field black, thorax dirty-dark-brown, darker marginally. Clusters of white hairs behind posterior eyes. Abdomen grey-brown, darkening

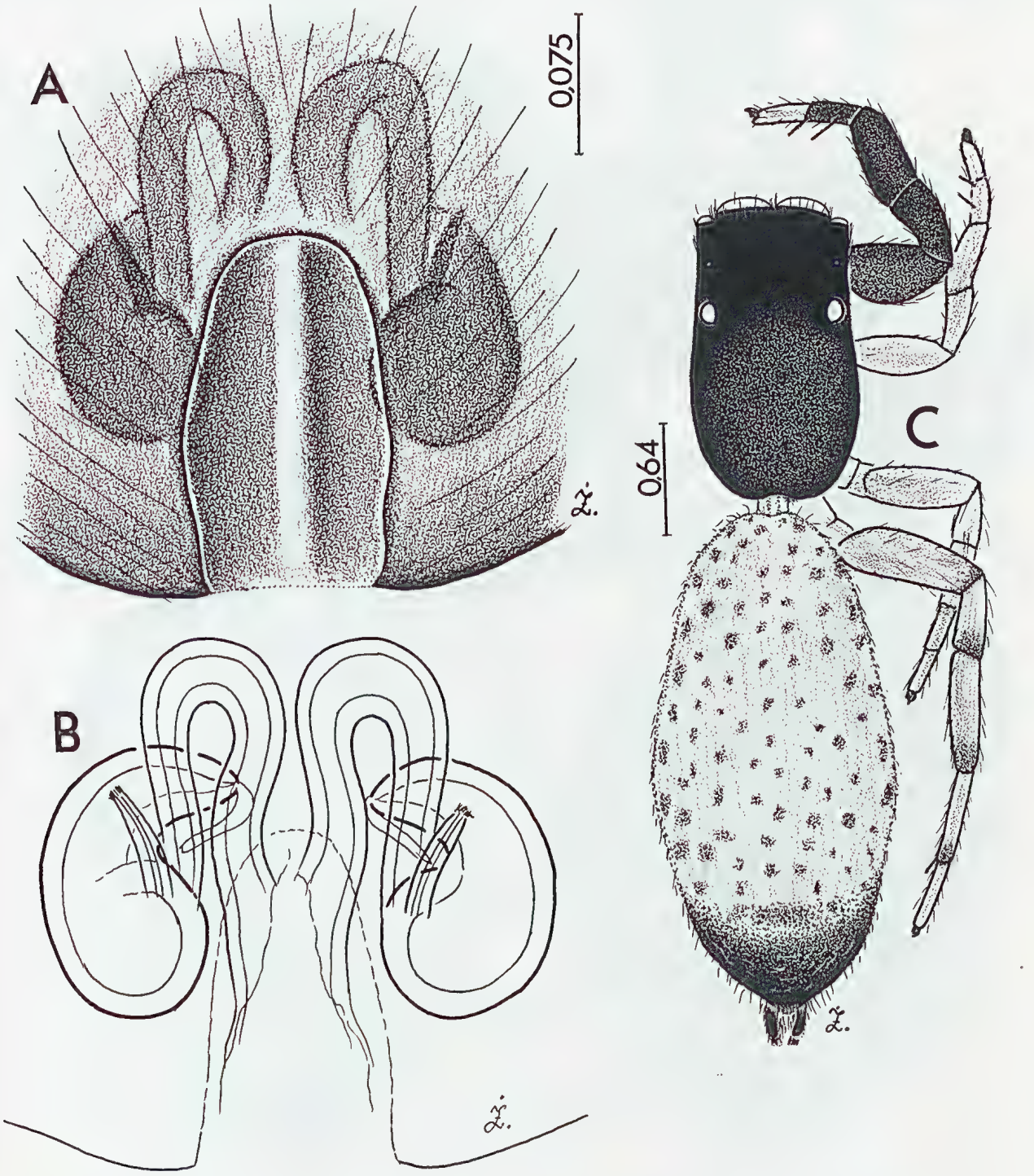



**Fig.49.** *Holoplatys panthera*, female (allotype).

posteriorly, with spots of white hairs. Clypeus blackish with single grey hairs. Chelicerae brown, pedipalps grey, lighter distally. Maxillae, labium and sternum dirty-orange-brown, the first with lighter tips. Venter light-grey centrally, laterally darker. Legs dirty-brown, lightening distally, tarsi yellow.

Epigyne (Fig.50B,C) with posterior depression, insemination ducts vast and long, narrowing distally, spermathecae long, accessory glands rather short.

*Leg spination.* mI: p1-1, r1-1.

*Dimensions.* CL 1.30, CW 0.81, CW/CL 0.62, EFL 0.45, EFL/CL 0.34, AEW 0.65, PEW 0.67, AL 2.11.

### *Holoplatys queenslandica* n.sp.

Figs 51-52, Map 8

**Material examined.** Queensland: HOLOTYPE, male, Hammond Island, Torres Strait, grassland along beach, 27 Feb. 1975, E. Cameron QMB S3554: ALLOTYPE, female, Black Mountain, summer 1971-72, N.C. Coleman, QMB S3576; PARATYPE, female, Rochedale S.F., beating, 7 Dec. 1979, V. Davies, R. Raven, QMB S6761. Papua New Guinea: PARATYPES 2 females, National Capital District, Waigani, Botanic Garden, under *Eucalyptus* bark, 28 June-

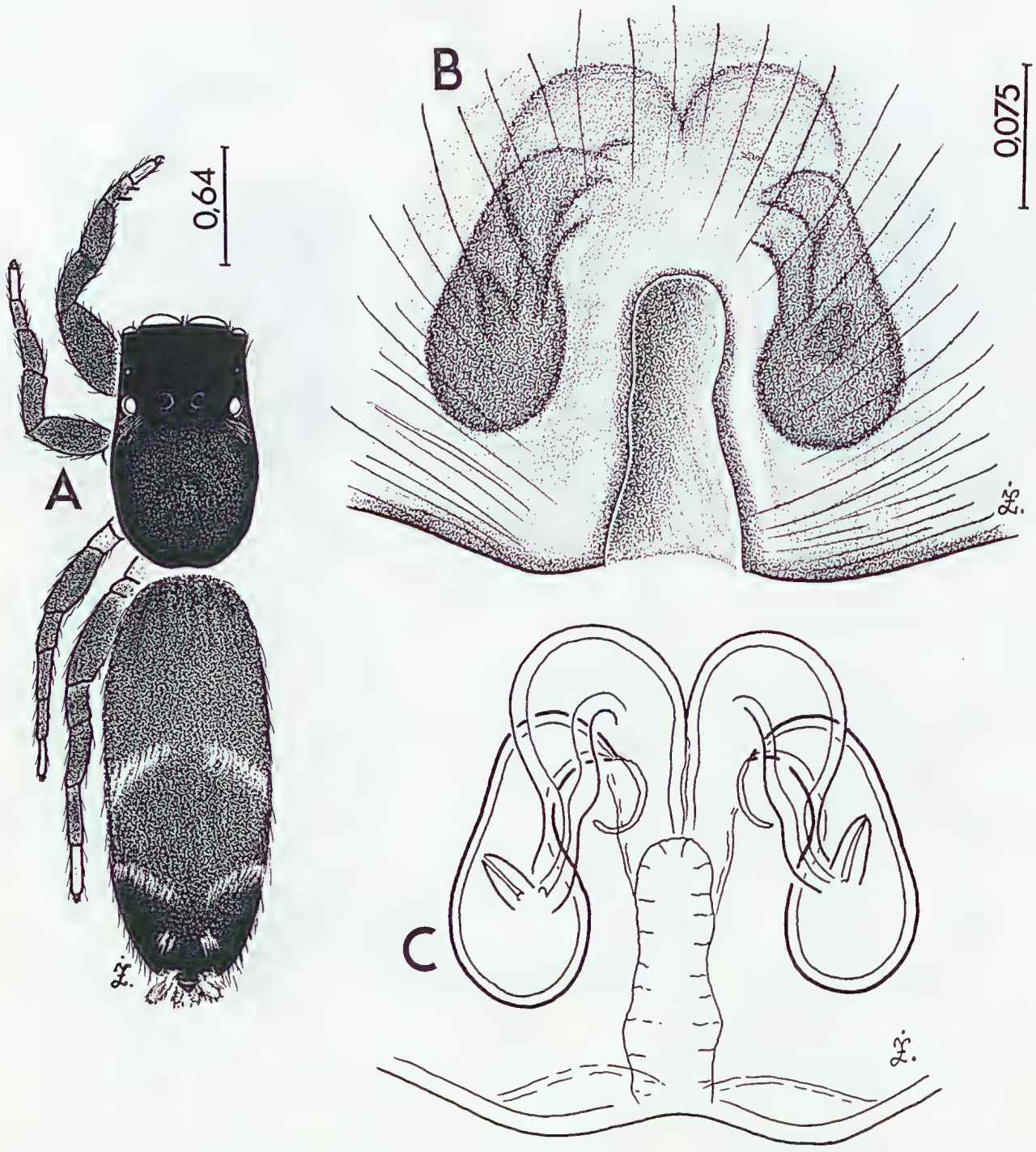



**Fig.50.** *Holoplatys minuta*, female (holotype).

1 July 1988, D. Court, M. Zabka, AMS KS19018.

**Diagnosis.** Thorax very elongate, dark. Female legs contrasting light. Distal spines only on metatarsus I. Dorsal tibial apophysis long, insemination ducts "C"-shaped, shorter than in other species of the group.

**Male** (Fig.51A). Eye field black, thorax dirty-brown, darker marginally. Abdomen grey-brown with anterior

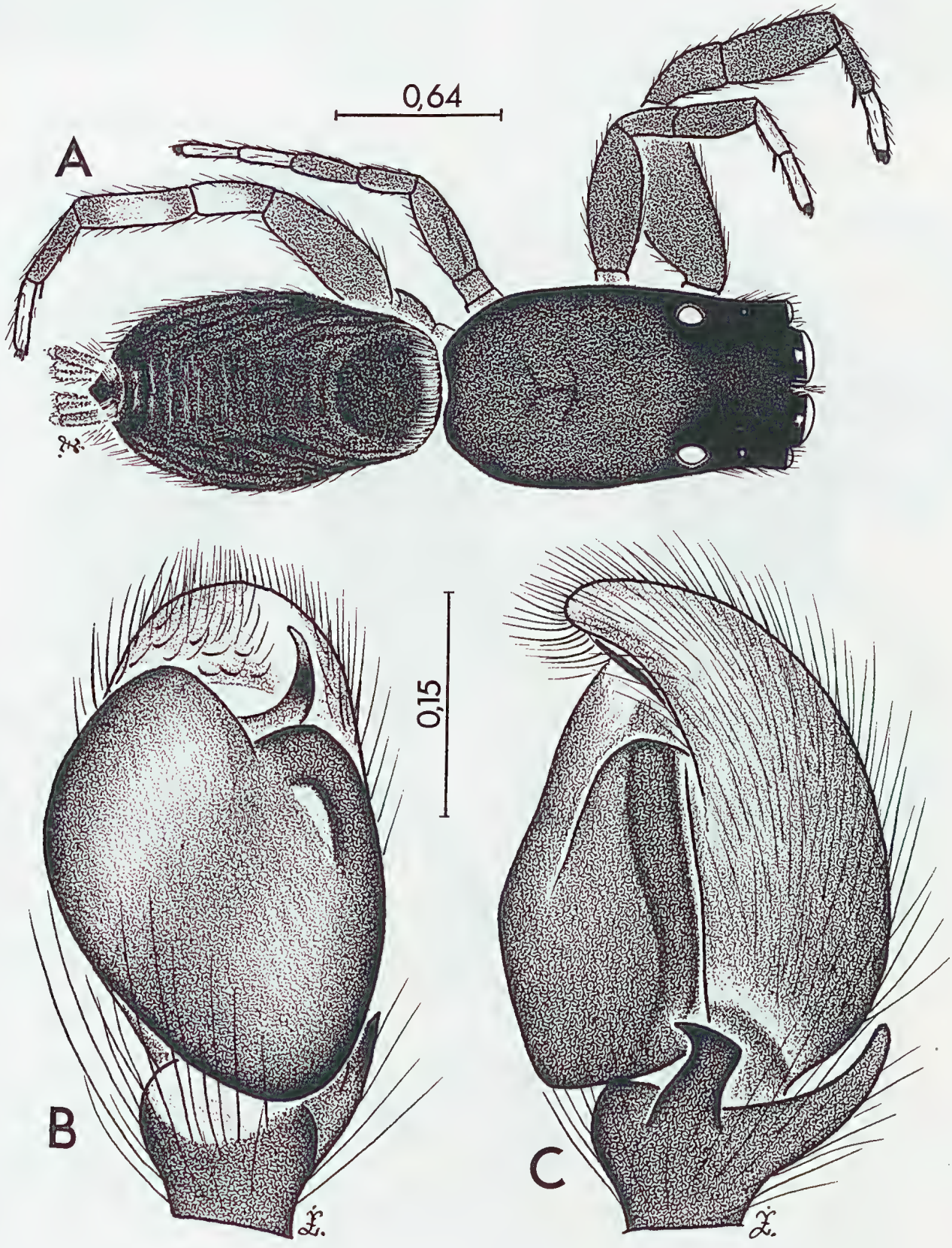



**Fig.51.** *Holoplatys queenslandica*, male (holotype).

brown scutum, lighter pattern of stripes and clusters of white hairs anteriorly and distally. Spinnerets dirty-orange. Clypeus black with single light hairs. Chelicerae, maxillae, labium and sternum dirty-orange-brown, the last with darker margin. Venter grey. Legs I and II dirty-brown, lighter dorsoventrally and distally, other legs slightly lighter.

Palpal organ (Fig.51B,C). Tegulum large, embolus short, thick, dorsal tibial apophysis long.

*Leg spination.* mI: p0-1, r0-1; mII: p0-1.

*Dimensions.* CL 1.43, CW 0.84, CW/CL 0.58, EFL 0.43, EFL/CL 0.30, AEW 0.65, PEW 0.66, AL 1.33.

**Female** (Fig.52A). Cephalothorax as in male. Abdomen dark-grey with clusters of light hairs anteriorly and distally. Spinnerets grey. Clypeus black with single grey hairs. Chelicerae, maxillae and labium grey, pedipalps yellow, sternum orange-brown with brown margin. Venter grey. Legs contrasting yellow-orange, sometimes femora slightly darker.

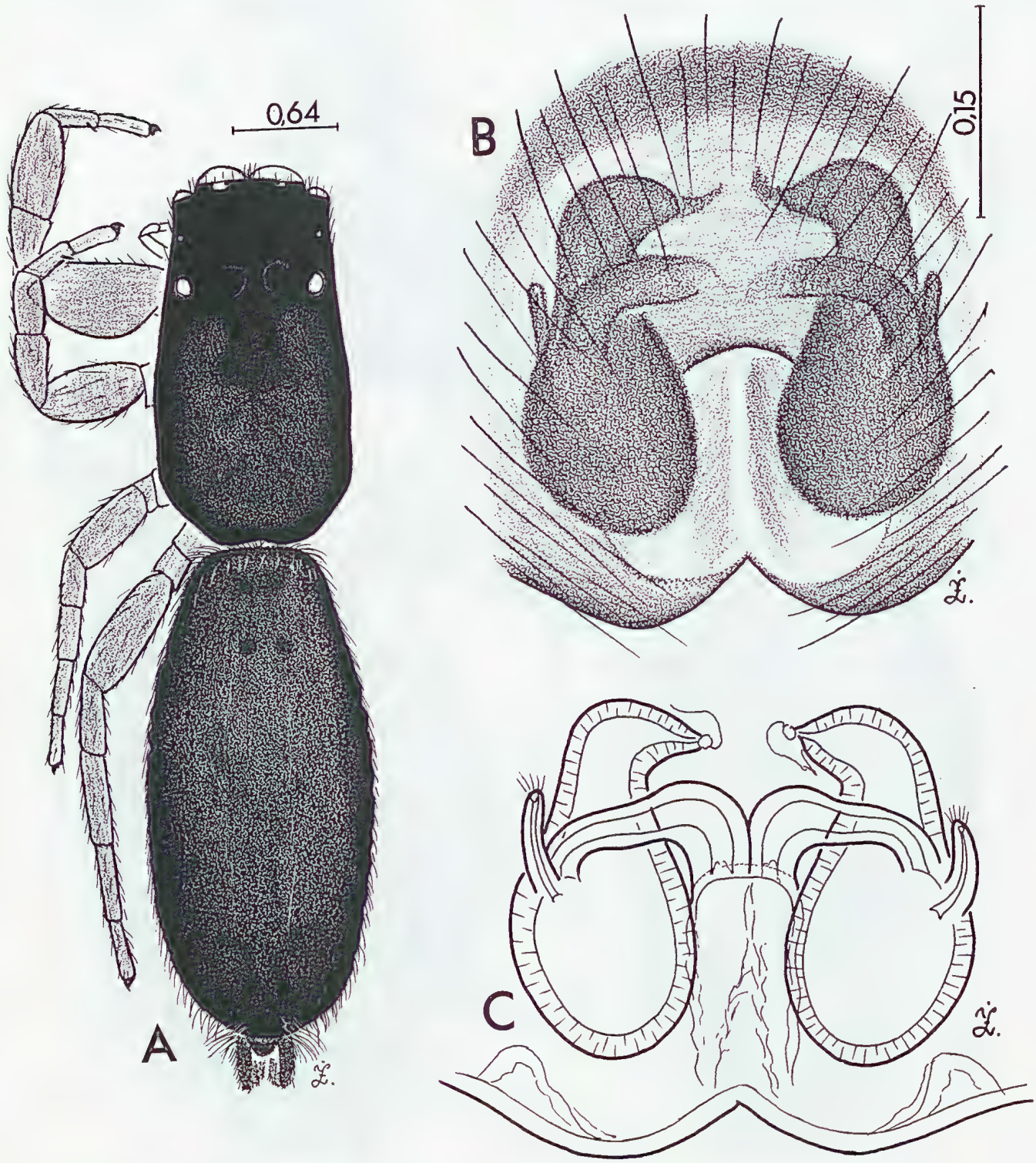



**Fig.52.** *Holoplatys queenslandica*, female (allotype).

Genitalia (Fig.52B,C). Insemination ducts 'C'-shaped, much shorter than in 2 previous species.

*Leg spination.* mI: p0-1, r0-1; MII: p0-1.

*Dimensions.* CL 1.68-2.21 (1.91), CW 0.99-1.25 (1.07), CW/CL 0.55-0.58 (0.56), EFL 0.53-0.60 (0.55), EFL/CL 0.27-0.31 (0.29), AEW 0.79-0.96 (0.85), PEW 0.79-0.99 (0.86), AL 2.04-2.97 (2.40).

## The *bicolor* Group (incertae sedis)

The group consists of two species recorded from single localitites in Queensland and Western Australia. Medium spiders (4.92-6.20). Cephalothorax higher than in other groups, bicolourous. Palpal organ similar to that in *panthera* and *grassalis* groups, but no dorsal apophysis on tibia. *Holoplatys bicolor* Sim. with tibial spines on legs I. The untypical body structure of these two species makes their inclusion with any of the above species groups unlikely and their generic status uncertain. Species included: *bicolor, bicoloroides.*

### *Holoplatys bicolor* Simon

Figs 53-54, Map 8

*Holoplatys bicolor* Simon, 1901b: 159.

**Material examined.** Queensland: type (?): female, Cooktown, MNHN 19924; male, Mount Molloy, grazed sclerophyll, 6 Nov. 1975, V.E. Davies, R. Raven, QMB S3593. Western Australia: male, Mitchell Plateau, Mining Camp, 9-19 May 1983, I. Naumann, J. Cardale, ANIC.

The only female from Cooktown longer than the dimensions given by Simon (5.08 and 4 respectively) therefore its type status is uncertain.

**Diagnosis.** Cephalothorax and abdomen bicoloured. Insemination ducts broad, copulatory openings oriented towards epigastric furrow. Tibial spines on legs I present.

**Male** (Fig.53A). Eye field dark with 2 black spots, thorax contrasting yellow. Abdomen lighter anteriorly, posteriorly black. In WA specimen (Fig.53B) whole abdomen almost black. Spinnerets dark-grey. Clypeus orange to dark. Chelicerae, pedipalps, maxillae and labium orange, sternum lighter, venter darker. Legs (Fig.53C,D) yellow to orange.

Palpal organ (Fig.53E,F) with small lateral apophysis on tibia. Tegulum elongate, with posterior lobe.

*Leg spination.* tI: p1-1 (2-2); mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 1.98, CW 1.15-1.19 (1.17), CW/CL 0.58-0.60 (0.59), EFL, 0.60, EFL/CL 0.33, AEW 0.79, PEW 0.85, AL 2.37-2.44 (2.40).

**Female** (Fig.54A). Body form and colour pattern similar to that in male. Clypeus, maxillae and labium orange, chelicerae, pedipalps and sternum lighter. Venter as dorsal aspect. Legs yellow to orange.

Genitalia as illustrated in Figure 54B,C.

*Leg spination.* tI: p1-1, r1-0; mII: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.31, CW 1.38, CW/CL 0.59, EFL 0.72, EFL/CL 0.31, AEW 0.92, PEW 0.97, AL 2.77.

### *Holoplatys bicoloroides* n.sp.

Fig.55, Map 8

**Material examined.** Western Australia: HOLOTYPE, female, Walsh Point, Admiralty Gulf, 16 May 1983, J. Balderson, ANIC.

**Diagnosis.** No spines on tibia I, insemination ducts shorter than in *bicolor*, abdomen uniformly dark.

**Male.** The male is unknown.

**Female** (Fig.55A). Eye field black, thorax yellow, darkening marginally. Abdomen black. Chelicerae, maxillae and labium brown, sternum and legs yellow, venter almost black.

Genitalia (Fig.55B,C) similar to *bicolor* but insemination ducts shorter, copulatory openings oriented towards each other.

*Leg spination.* mI: p0-1, r0-1.

*Dimensions.* CL 2.57, CW 1.42, CW/CL 0.55, EFL 0.79, EFL/CL 0.30, AEW 1.12, PEW 1.12, AL 3.63.

## The *invenusta* Group (incertae sedis)

The group consists of two relatively large species (6.30-10.23) known from scattered localities in Queensland, New South Wales, Victoria and Western Australia. Palpal organs with lateral and dorsolateral tibial apophyses, cymbium with flange. Copulatory openings close each other, insemination ducts short and vast, spermathecae very large. Femora of legs darker than other segments. Species included: *invenusta, borali.*

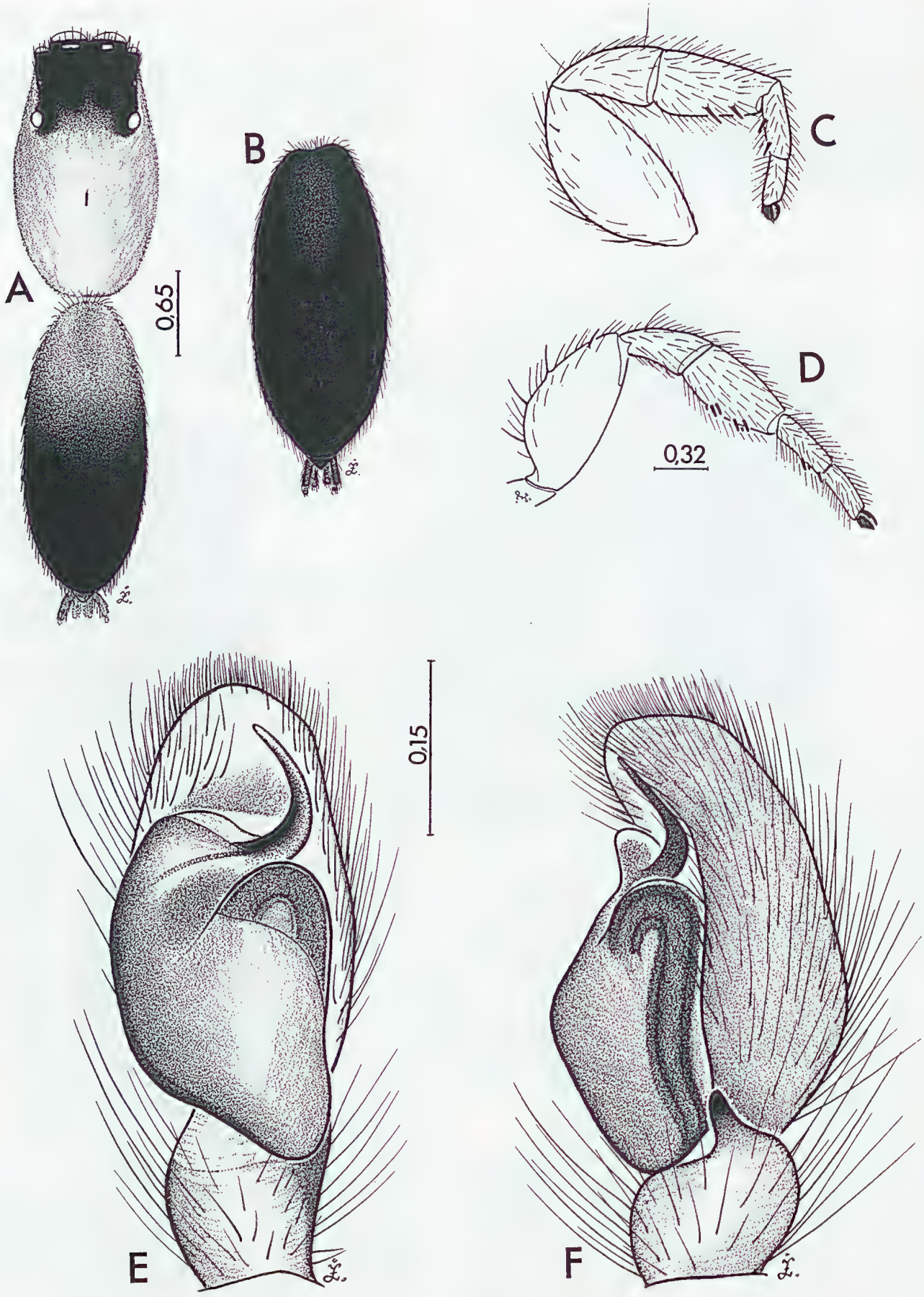



**Fig.53.** *Holoplatys bicolor*, male: dorsal body, abdomen, legs I and palpal organ (A,D-F specimen from Mount Molloy, B,C specimen from Mitchell Plateau).

***Holoplatys invenusta*** (L. Koch) n.comb.

Figs 56-57, Map 9

*Marptusa invenusta* L. Koch, 1879: 1099.
*Ocrisiona invenusta*.–Simon, 1901a: 602.

**Material examined.** New South Wales: HOLOTYPE, female, Sydney, (Mus. Godeffroy 16524), ZMH. Queensland: female, Preston, 1978, T. Adams, QMB S3588; female, Endfield Station, 30 m west Westmar, 9 Jan. 1979, R. Raven, V. Davies, QMB S4601. Victoria: male, female, Melbourne, Ashburton, 5 Jan. 1988, P.K. Lillywhite, WAMP 89/272-3.

**Diagnosis.** Cymbium of male palpal organ with

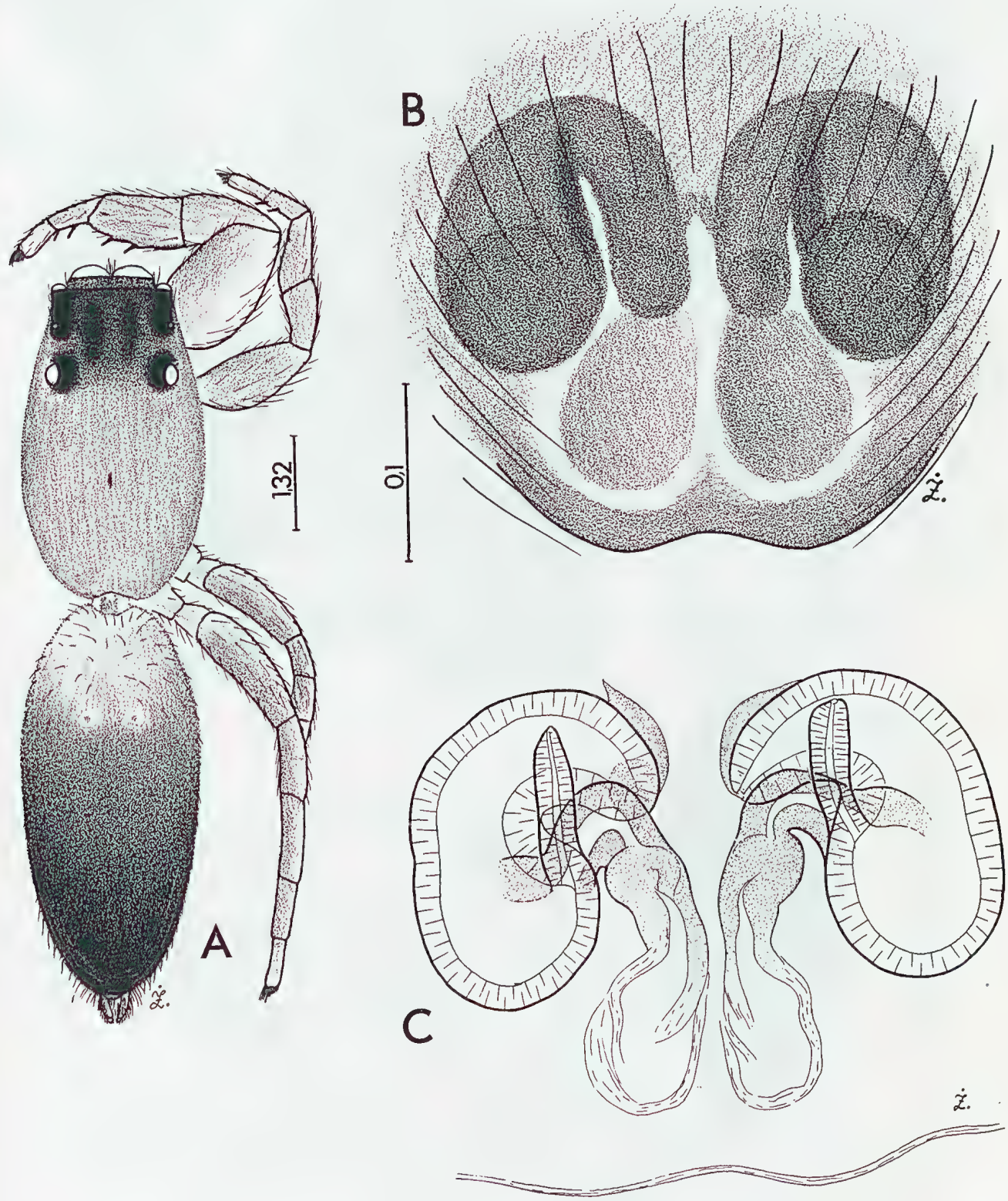



**Fig.54.** *Holoplatys bicolor*, female (type?).

flange (see arrow), tibial apophyses hook-like. Posterior margin of epigyne 'W'-shaped.

**Male** (Fig.56A). Eye field dark with 2 longitudinal black spots, thorax slightly lighter with black margin. Whole surface with white and dark hairs. Abdomen brownish-grey with light transverse spots and delicate, orange anterior scutum. Spinnerets grey-brown. Clypeus brown-black. Chelicerae, maxillae and labium brown with lighter tips, sternum brown, venter grey-brown.

Palpal organ as illustrated in Figure 56B,C.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 2.90, CW 1.80, CW/CL 0.62, EFL 1.00, EFL/CL 0.34, AEW 1.50, PEW 1.50, AL 3.40.

**Female** (Fig.57A). Cephalothorax brown to dark-brown, abdomen dark-grey with light mosaic of lines and small spots. Clypeus and chelicerae brown, maxillae and labium lighter with yellow tips, sternum orange, venter beige. Femora of legs brown, lighter dorsoventrally, other segments orange.

Epigyne (Fig.57B-D) with 'W'-shaped posterior margin. Insemination ducts short. Copulatory openings in the central part of epigyne, close each other. Spermathecae large.

*Leg spination.* mI: p1-0, r1-1; mII: p1-1.

*Dimensions.* CL 3.10-4.20 (3.83), CW 1.95-2.70 (2.45), CW/CL 0.62-0.63 (0.63), EFL 1.05-1.30 (1.19), EFL/CL 0.32-0.33 (0.33), AEW 1.75-2.10 (1.93), PEW 1.65-2.10 (1.88), AL 4.60-5.70 (5.23).

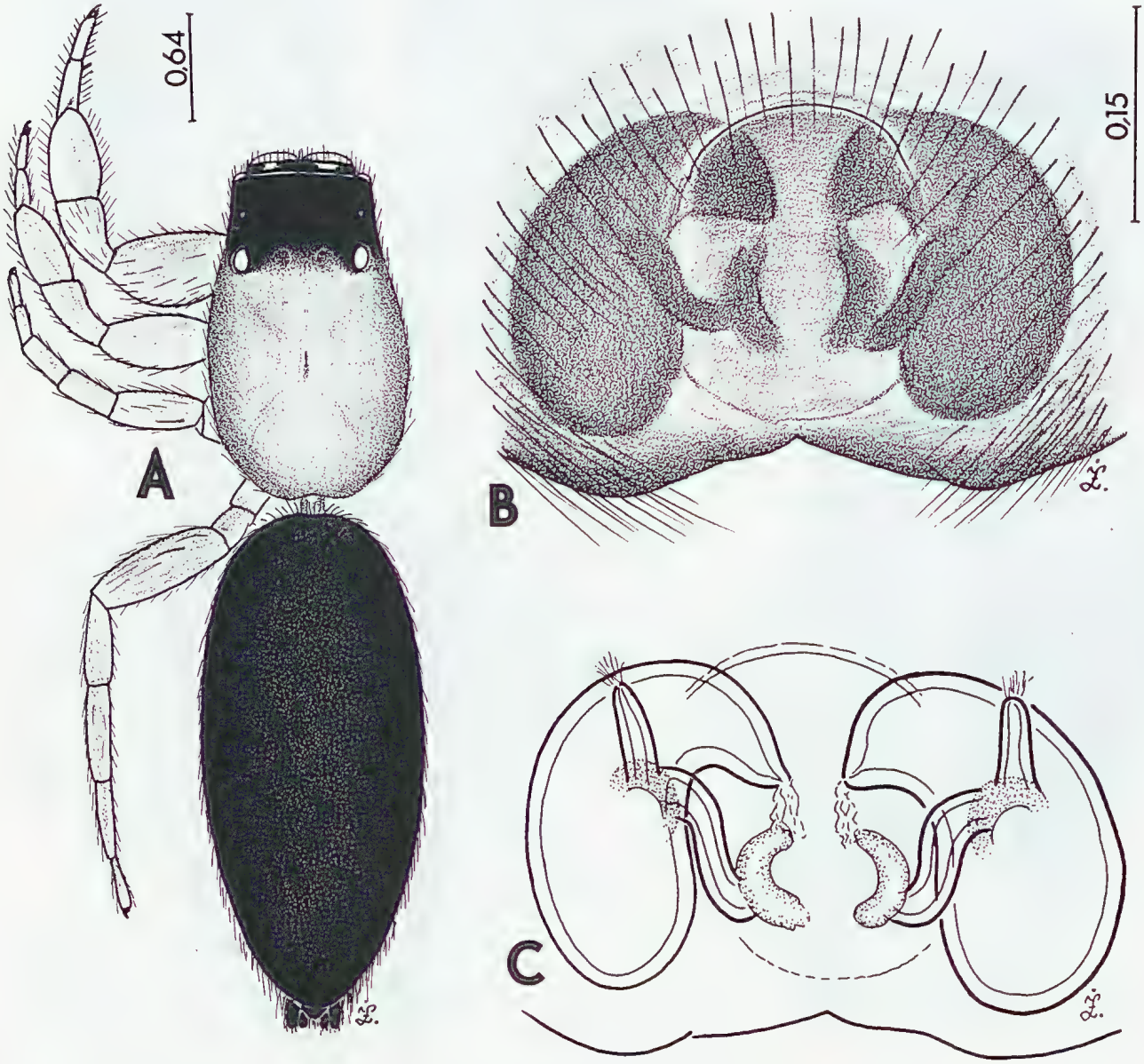



**Fig.55.** *Holoplatys bicoloroides*, female (holotype).

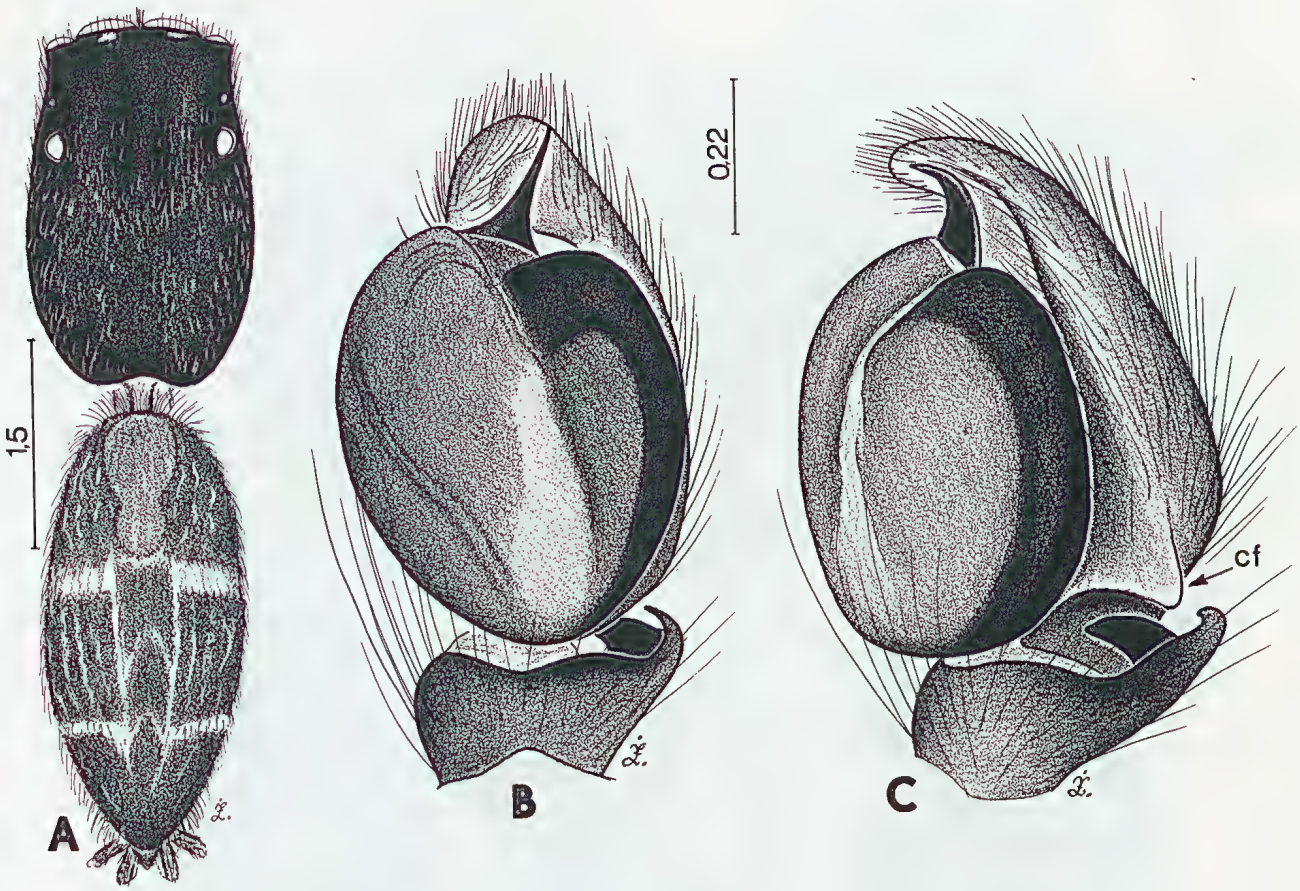
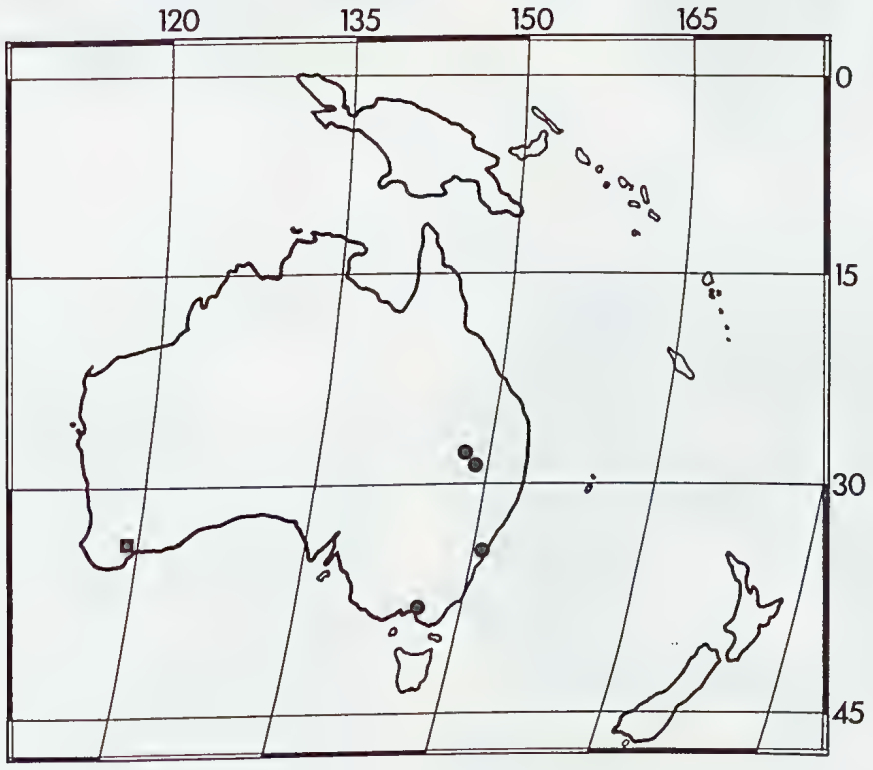



**Fig.56.** *Holoplatys invenusta*, male.




Map 9. Closed circle – *Holoplatys invenusta* (L. Koch); closed square – *H. borali* n.sp.

### *Holoplatys borali* n.sp.

Fig.58, Map 9

**Material examined.** Western Australia: HOLOTYPE, female, Fitzgerald River Reserve, 7 Jan. 1971, L. Koch, W.K. Youngson, WAMP 88/37.

**Diagnosis.** Structure of genitalia similar to *invenusta* but posterior margin of epigyne with double pocket instead of 'W'-shaped.

**Male.** The male is unknown.

**Female** (Fig.58A). Eye field black, thorax dark-brown, with brown and whitish hairs marginally. Abdomen partly macerated, dark-grey with lighter spots. Spinnerets dark-grey. Clypeus black with brown hairs. Chelicerae brown, maxillae lighter with yellow tips, labium and sternum light-brown with darker margin. Venter grey, darker laterally. Femora of legs and pedipalps brown, other segments yellow. Leg I generally darker than others.

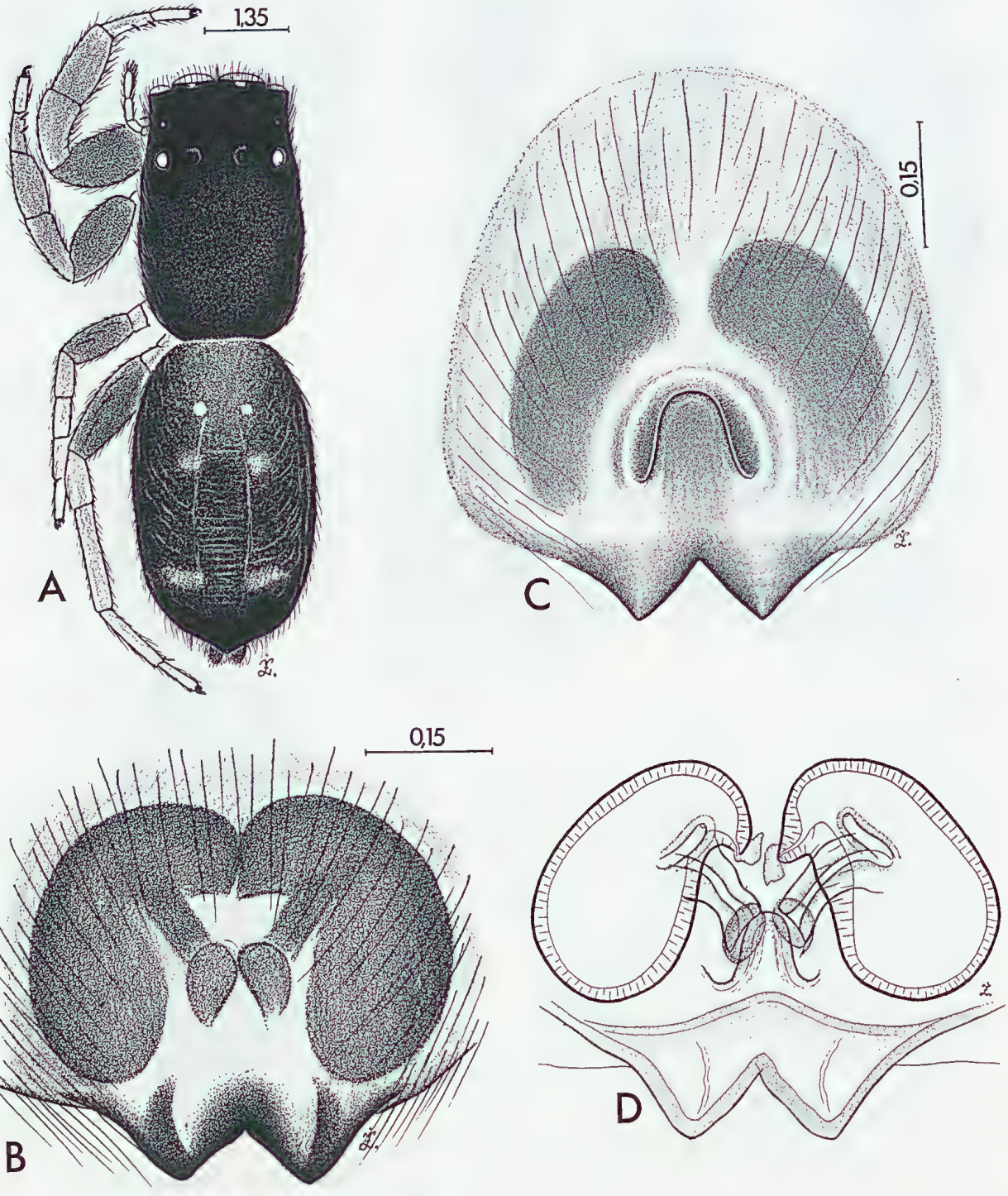



**Fig.57.** *Holoplatys invenusta*, female (A,B - specimen from Preston, C,D - holotype).

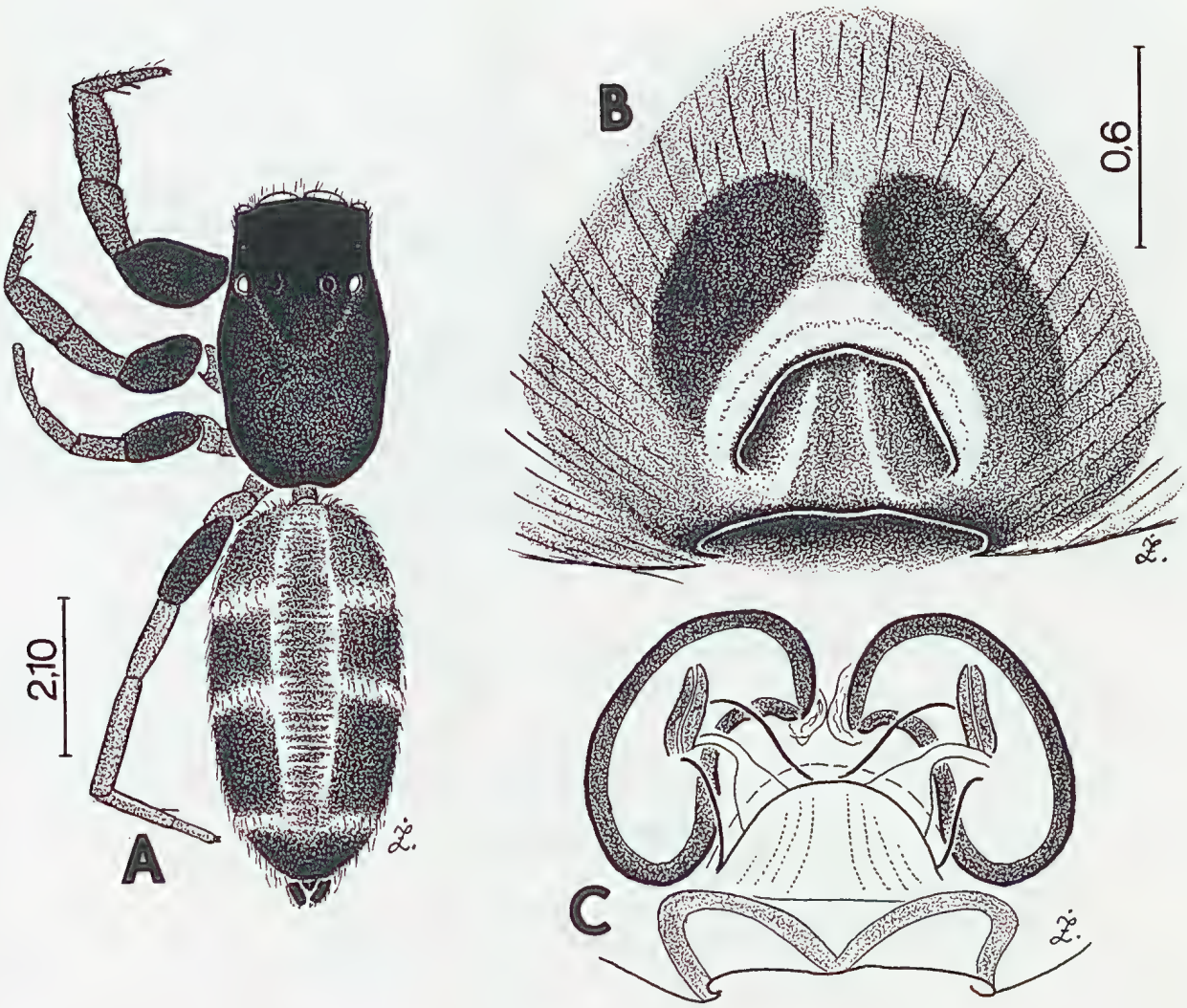



**Fig.58.** *Holoplatys borali*, female (holotype).

Genitalia as in Figure 58B,C.

*Leg spination.* mI: p1-1, r1-1; mII: p1-1.

*Dimensions.* CL 4.29, CW 2.71, CW/CL 0.63, EFL 1.25, EFL/CL 0.29, AEW 2.04, PEW 1.98, AL 5.94.

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# *Perinereis* (Polychaeta, Nereididae) from Australia, with Redescriptions of Six Additional Species

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ABSTRACT. The genus *Perinereis*, with 56 species worldwide, is represented in Australian waters by 15 species. Eleven Australian species with one or two bars on Area VI are described, and six species not recorded from Australia are redescribed from type material. No new species are described. A key is provided to all 15 Australian species of *Perinereis*. A list of all species of *Perinereis* is provided in an appendix.

HUTCHINGS, P.A., A. REID & R.S. WILSON, 1991. *Perinereis* (Polychaeta, Nereididae) from Australia, with redescriptions of six additional species. Records of the Australian Museum 43(3): 241–274.

The genus *Perinereis*, comprising 56 species and nominal subspecific forms, is usually informally subdivided on the basis of the number of smooth bar-shaped paragnaths on Area VI of the pharynx. Appendix 1 lists all known species of *Perinereis*, arranged in an informal grouping of similar species. This paper treats 11 Australian species which possess either one or two bars on each side of Area VI (Groups 1 and 2). Six additional species of *Perinereis* with this arrangement of bar-shaped paragnaths on Area VI, but not recorded from Australia are redescribed from type material. Species of *Perinereis* characterised by a distinctive arc of short bars on Area VI (usually numbering 6-14 on each side) (Group 3), and comprising 20 nominal forms worldwide, are revised by Wilson & Glasby (in preparation). A key is provided to all 15 Australian species of *Perinereis*, including those described elsewhere by Wilson & Glasby (in preparation).

This paper is the third in a series describing Australian Nereididae; earlier papers treat the subfamily Gymnonereidinae (Hutchings & Reid, 1990), and the genera *Leonnates*, *Platynereis* and *Solomonereis* (Hutchings & Reid, 1991).

## Materials and Methods

This study is based on all available nereidid collections from all Australian State museums. Terminology follows Hutchings & Reid (1990). Largest and smallest specimens in a range are chosen from width measurements. Widths are given as two figures; the first is the width excluding parapodia and the second (in parentheses) if given, refers to the width including parapodia. Synonymies include records from the literature not all of which have been checked against original material, but no new synonymies have been included unless type material has been examined. We felt that in this revisionary paper it would be helpful to include all the previous synonomies as they have never all been published together before. Australian distributions are based on material examined here unless indicated otherwise in the text. Non-Australian distributions are largely based on the literature, however, where overseas material has been examined this is marked with an asterisk. Institution codes referred to are as follows: AM – Australian Museum, Sydney; BM – British Museum (Natural History), London, UK; HZM – Hamburg Zoological Museum, Hamburg, FDR; NMV – Museum of Victoria, Melbourne; NTM – Northern Territory Museum of Arts & Sciences, Darwin; QM – Queensland Museum, Brisbane; SAM – South Australian Museum, Adelaide; TASM – Tasmanian Museum & Art Gallery, Hobart; WAM – Western Australian Museum, Perth; WMNH – Wroclaw University Museum of Natural History, Poland.

All species are figured and all parapodia figured are anterior views.

## Taxonomic Characters

Species of *Perinereis* possess a number of qualitative and quantitative characters, some of which have not been made use of in earlier taxonomic studies. The two principal qualitative characters used in the key below are the presence of smooth bars on Area IV of the pharynx and expansion of the dorsal notopodial lobe. These characters also form the basis of an informal species grouping presented in the Appendix. The subdivision of the genus is an artificial scheme intended only to facilitate species-level comparisons and should not be taken to imply phylogenetic relationships.

The primary qualitative character used is the presence of smooth parallel bar shaped paragnaths (in addition to the usual cones) on Area IV of the pharynx. This character was used to distinguish species of *Neanthes* by Wilson (1984) and in the *Perinereis nuntia* species group by Wilson (in preparation) and Wilson & Glasby (in preparation) but is not mentioned in earlier descriptions. In most species, however, presence/absence of bars on Area IV is a constant and useful character. Only *P. camiguinoides*, *P. pseudocamiguina*

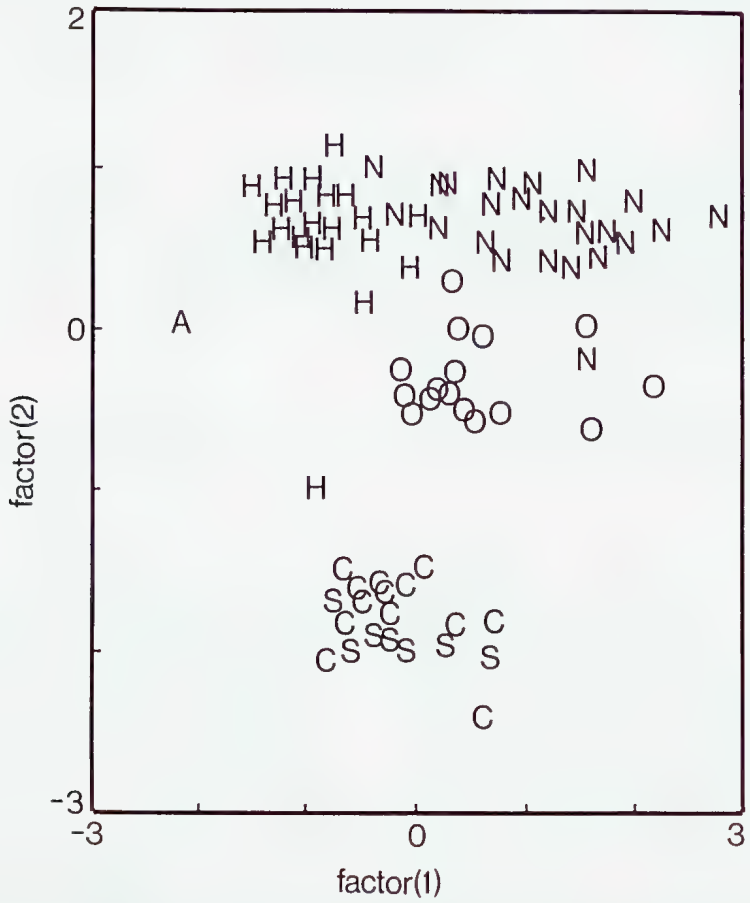


**Fig.1.** Plot of principal components scores of *Perinereis* spp. with one bar on Area VI. A = *P. amblyodonta*; C = *P. calmani*; H = *P. helleri*; N = *P. nigropunctata*; O = *P. obfuscata*; S = *P. seurati*.

and *P. variodentata* are polymorphic in this respect. The bars on Area IV are usually conspicuous; they are illustrated below in the figure of *P. amblyodonta*.

Expansion of the dorsal notopodial lobe on posterior setigers has been used by most authors to distinguish species. Assessment of the degree of expansion of the dorsal notopodial lobe requires some guide, as there is slight expansion of this lobe posteriorly in most species. By our standards, a specimen is described as having a greatly expanded dorsal notopodial lobe posteriorly only if the dorsal lobe is more than two times as long as the ventral lobe and has the dorsal cirrus tending to be terminally attached (this will usually only be evident in the posteriormost 10-30 setigers). Comparison of dubious specimens with figures referred to in the descriptive accounts below of species with expanded notopodial lobes (e.g., *P. amblyodonta*, Fig.3) and species with unmodified notopodial lobes (e.g., *P. aibuhitensis*, Fig.2) should make this distinction clear. Incomplete or epitokous specimens may, however, be impossible to determine. For a diagram of the structure of the parapodia with all the lobes labelled see Figure 1 in Hutchings & Reid (1990).

Absence of heterogomph spinigers from the ventral neuropodial fascicle in a variable number of anterior setigers is another qualitative character that is evident in some species. This character shows considerable intraspecific variability but may be useful in some instances.

## Statistical Analysis

Guidelines for the use of quantitative characters, paragnath counts, in the genus *Perinereis* will be provided by Wilson (in preparation), and are followed here. In univariate comparisons based on each Area of the pharynx, species level differences are only indicated if populations do not (or barely) overlap in paragnath counts. Statistically 'significant' differences alone do not imply the presence of distinct species. Multivariate comparisons (based on counts for all Areas of the pharynx) can be used to indicate species level discrimination if populations are plotted as discrete clusters of points in multivariate space. Wilson (in preparation) is using canonical variates analysis (= multiple discriminant analysis) to compare populations in the absence of *a priori* species determinations. In this paper we have used principal components analysis (PCA), which does not make use of *a priori* designations of groups of specimens, to confirm differences between those Australian species most likely to be confused. These species (with only 1 bar in Area VI; *P. amblyodonta*, *P. calmani*, *P. helleri*, *P. nigropunctata*, *P. obfuscata* and *P. suluana*) are distinguished in the key below using qualitative characters which may be impossible to assess in incomplete material (e.g., expansion of notopodial lobe). PCA of these species based on the quantitative data alone (paragnath counts) confirms the significance of qualitative differences and enables the quantitative data to be summarised in fewer dimensions. The PCA was performed on raw paragnath data of samples of 20 to 30 specimens of each species. The resultant plot of extracted factor scores (Fig.1) separates all species with the exception of *P. calmani* and *P. suluana*. These two species however are distinguished by the absence of paragnaths in Areas VII-VIII and very distinct dorsal pigmentation pattern in *P. suluana* (*P. calmani* has 10-13 paragnaths on VII-VIII) and we retain these as distinct species. The plot of PCA factor scores, and factor score coefficients (Table 1), provide means of estimating the importance of counts for each Area in distinguishing species. Thus, *P. helleri*, *P. obfuscata* and *P. calmani* are separated primarily along factor 2. Table 1 records the highest coefficients for factor 2 as the oral ring Areas V and VII-VIII; counts for these Areas are therefore more taxonomically useful in distinguishing these species. Similarly, factor 1, on which the maxillary ring paragnaths I, II and IV load most strongly, best separates *P. helleri* and *P. nigropunctata*.

Table 1. Factor score coefficients from principal components analysis of Australian *Perinereis* species with 1 bar on Area VI.

| | factors | | |
|---|---|---|---|
| | 1 | 2 | 3 |
| I | 0.476 | 0.084 | - 0.349 |
| IIL | 0.415 | - 0.156 | - 0.121 |
| IIR | 0.432 | - 0.182 | - 0.127 |
| III | 0.143 | 0.140 | 0.028 |
| IVLC | - 0.293 | - 0.050 | 0.663 |
| IVRC | - 0.363 | - 0.033 | 0.730 |
| V | - 0.259 | 0.612 | 0.039 |
| VII-VIII | 0.121 | 0.423 | - 0.181 |

## Key to Australian Species of *Perinereis*

1. Area VI with 1 bar ..... 2

—— Area VI with 2 bars ..... 8

—— Area VI with more than 2 bars ..... 11

2. Area IV with smooth bars in addition to cones ..... 3

—— Area IV with cones only ..... 4

3. Area III with fewer than 10 cones; VII-VIII usually more than 50; expanded dorsal notopodial ligule dorsally convex (Fig.4d) ..... *P. barbara*

—— Area III with more than 10 cones; VII-VIII usually with fewer than 50; expanded dorsal notopodial ligule strap-like, dorsally straight (Fig.3f) ..... *P. amblyodonta*

4. Dorsal notopodial lobe greatly expanded posteriorly (Fig.10c) ..... 5

—— Dorsal notopodial lobe not greatly expanded posteriorly (Fig.9b) ..... 7

5. Area VII-VIII bare ..... *P. suluana*

—— Area VII-VIII with paragnaths ..... 6

6. Area V with 3 paragnaths (rarely 1) ..... *P. nigropunctata*

—— Area V with 1 paragnath (rarely 2) ..... *P. obfuscata*

7. Areas III and VII-VIII with fewer than 14 paragnaths ..... *P. calmani*

—— Area III with more than 14 paragnaths; VII-VIII with more than 20 paragnaths ..... *P. helleri*

8. Dorsal notopodial lobe reduced posteriorly (Fig.2d) ..... *P. aibuhitensis*

—— Dorsal notopodial lobe slightly expanded posteriorly (Fig.18b), dorsal cirrus becoming distally inserted on posteriormost setigers ..... 9

9. Area I with more than 3 paragnaths; III with fewer than 7; bars usually present on IV ..... *P. variodentata*

—— Area I with fewer than 4 paragnaths; III with many more than 6; bars absent on IV ..... 10

10. Area IV with more than 39 paragnaths; VII-VIII with more than 57 ..... *P. vancaurica*

—— Area IV with fewer than 37 paragnaths; VII-VIII with fewer than 57 ..... *Perinereis singaporiensis*

11. Bars present on Area IV of pharynx ..... 12

—— Bars not present on Area IV of pharynx ..... 13

12. Area VI with fewer than 10 bars (usually 6-8) ..... *P.* sp A*

—— Area VI with more than 10 bars (usually 12-16) ..... *P. vallata**

13. Areas I and II without paragnaths ..... *P. caeruleis**

—— Areas I and II with paragnaths ..... *P. nuntia**

* see Wilson & Glasby (in preparation) for descriptions.

## *Perinereis* Kinberg

*Perinereis* Kinberg, 1866: 175-176.

**Type species.** *Perinereis novaehollandiae* Kinberg, 1866, by original designation.

**Diagnosis.** Two pairs of eyes, 1 pair of antennae, 1 pair of palps, 4 pairs of tentacular cirri. Pharynx with conical paragnaths on maxillary ring or both rings. Transverse bars on Area VI. First 2 parapodia uniramous, subsequent parapodia biramous. Notopodia with homogomph spinigers, neuropodia with homogomph and heterogomph spinigers and heterogomph falcigers (after Fauchald, 1977).

**Comments.** The presence of smooth bar-shaped paragnaths on Area VI serves to diagnose the genus. In *Perinereis aibuhitensis* and *P. suluana* the bars on Area VI are so short as to appear cone-like in some specimens, however, most specimens possess very short bars on Area VI. Care must be taken with these species, which could be incorrectly identified as species of *Neanthes* if sufficient comparative material is not available.

Bar-shaped paragnaths are also found on Area IV (in addition to cones) in some species.

## *Perinereis aibuhitensis* (Grube)

Fig.2a-e

*Nereis* (*Perinereis*) *aibuhitensis* Grube, 1878: 89-90, pl.5, fig.3.–Horst, 1924: 168-169, pl.33, figs 4-6.
*Perinereis aibuhitensis*.–Fauvel, 1932: 106.–Fauvel, 1953: 209-210, fig.107a.–Russell, 1962: 6-7.–Wu *et al.*, 1985: 189-193.–Hylleberg & Nateewathana, 1986: 3-5, fig.2A-Q.
*Nereis aibuhitensis*.–Monro, 1934: 361-362.
*Neanthes linea* Treadwell, 1936: 268-270, fig.19a-e (fide Hartman, 1938).
*Neanthes orientalis* Treadwell, 1936: 270-272, fig.19f-i (fide Hartman, 1938).

**Material examined.** Philippines: Aibuhit, no further data, 1 lectotype and paralectotype (not conspecific, see below; WMNH 302), 1 PARALECTOTYPE ZMB Q3440.

Non-type material. Australia: Western Australia – Admiralty Gulf, Port Warrender, 14°35'S 125°53'E, Oct. 1976, several (WAM 462-86), several (WAM W486-86); Willie Creek, 17°46'S 122°12'E, 2 Oct. 1984, 1 (NTM W2181); Broome, 17°58'S 122°13'E, 2 Oct. 1984, 1 (NTM W2298). Northern Territory – Port Essington, Victoria Settlement, 11°16'S 132°09'E, 12 Nov. 1985, 1 (NTM W3063), 1 (NTM W3278), 1 (NTM W3297), 1 (NTM W3308); Port Essington, Wangewanja Cove, 11°23'S 132°09'E, 13 Sept. 1985 (NTM W3336), (NTM W3340), 1 (NTM W3360), (NTM W3413), (NTM W3415); West Bay, 11°24'S 132°10'E, 14 Sept. 1985, 1 (NTM W3602); Port Essington, Mangrove Point, 11°24'S 132°11'E, 14 May 1983, 5 (NTM W1330), 15 Nov. 1985, 2 (NTM W3185), 1 (NTM W3192), 1 (NTM W3630); Adelaide River, 12°28'S 131°21'E, 22 May 1985, 1 (NTM W2787), 1 (NTM W2808), 21 May 1985, 1 (NTM W2951), 1 (NTM W2960), 22 May 1985, 1 (NTM W2985), 1 (NTM W2989), (NTM W2991), 1 (NTM W3000), 1 (NTM W3003), 23 May 1985, 1 (NTM W3008), 1 (NTM W3009); McArthur River, Black Rocks Landing, 15°53'S 136°35'E, 1 Aug. 1985, 1 (NTM W3736); Minimini Creek, 11°43'S 132°39'E, 19 June 1984 (NTM W1787), 1 (NTM W1789); Buchanan Island, 11°49'S 130°39'E (NTM W436), 18 Nov. 1982, 1 (NTM W438); Annesley Point, 11°24'S 132°51'E, 19 June 1984, 1 (NTM W1758); Darwin, East Arm, 12°30'S 130°55'E, 31 May 1984, 5 (NTM W1814), (NTM W1815), 2 (NTM W2054), 14 Dec. 1984, 1 (NTM W2510), 1 (NTM W2516), 1 (NTM W2523), 4 Feb. 1985, 1 (NTM W2660), 1 (NTM W2664), 1 (NTM W2670), 1 (NTM W2690), 1 (NTM W2692), 1 (NTM W2694), 1 July 1985 (NTM W2866); Wyndham, King River, 15°47'S 128°12'E, 21 Mar. 1985, 1 (NTM W2617). Queensland – Cairns, 16°55'S 145°46'E, 20 Nov. 1984, 1 (NTM W2350), 18 Nov. 1984, 4 (NTM W2376); Cribb Island, Jacksons Creek, 27°21'S 153°07'E, 20 Sept. 1972, 1 (QM G7518), Oct. 1972, 1 (QM G7549), 12 Dec. 1972, 2 (QM G7550), 1 (QM G7551), 1 (QM G7553).

**Description.** Material examined up to 100 mm length, 4 mm width, 0.6-2.5 mm jaw length, up to 124 setigers. Colour in alcohol, cream-yellow. Prostomium trapezoidal with faint median furrow. Eyes with distinct lenses. Broad, dome-shaped palps with small, rounded palpostyles, short, triangular antennae. Longest tentacular cirri, extending to setiger 3. Jaws robust, heavily sclerotised with 6-8 triangular teeth spread along entire cutting margin. Pharynx with conical paragnaths on both rings and smooth bars present on Area VI arranged as follows: I=1-4 (usually 2); II=6-14, III=12-34 in a patch, 2-5 (usually 2-3) laterally, separate from central patch, IV=8-23, V=3 (rarely 1), VI=2 very short 'bars', VII-VIII=37-48 in 3 irregular rows. Area IV without bars.

Anterior notopodia broad, with triangular dorsal ligules and slightly shorter, subtriangular median ligules, superior lobes reduced or absent. Dorsal cirrus triangular, slightly shorter than dorsal notopodial ligule (Figs 2a,b). Neuropodial lobes slightly longer than notopodial lobes, with indistinct superior lobe, low, rounded inferior and postsetal lobes. Ventral ligule conical. Ventral cirrus short, triangular, approximately half as long as neuropodial ligule. Median and posterior notopodia as for anterior notopodia with lobes reduced in size, triangular rather than conical in shape (Figs 2c,d). Dorsal notopodial ligule reduced in size in far posterior setigers with dorsal cirrus exceeding length of ligule.

Neurosetae with homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph falcigers (Fig.2e) and heterogomph spinigers in subacicular fascicle. Falcigers long bladed (Horst, 1924: pl.33, fig.5). Anal cirri long, tapering.

**Remarks.** The type material (WMNH 302) includes specimens of two species. One, which agrees well with Grube's original description, we have designated the

lectotype. The other specimen contains one bar only in Area VI and has not been identified to species. A paralectotype is also deposited in ZMB.

*Perinereis aibuhitensis* is most similar to *P. vancuarica* (Ehlers, 1868) but the two species can be distinguished on the basis of the bars in Area VI, which are very short in *P. aibuhitensis* but long in *P. vancuarica*. *Perinereis aibuhitensis* is also similar to *P. singaporiensis*, but differs in the following characters: *P. aibuhitensis* has short bars in Area VI, dorsal notopodial lobes reduced posteriorly, and has three rows of cones in Areas VII -VIII.

In some specimens of *Perinereis aibuhitensis* the bars in Area VI are so short as to be easily mistaken for cones and the material identified as a species of *Neanthes*. Such specimens would most likely be confused with *Neanthes vaalii* Kinberg, 1866, however, the presence of conspicuous bars in Area IV, notopodial presetal lobes and short bladed falciger in *N. vaalii* readily distinguish this species from P. *aibuhitensis*. In all other characters the Australian material is very similar to the designated lectotype (WMNH 302).

**Habitat.** Occurs in mangroves, among oyster encrusted rocks and rocky reef.

**Fig.2.** *Perinereis aibuhitensis* PARALECTOTYPE ZMB 3440. (a) parapodium 3; (b) parapodium 10; (c) parapodium 50; (d) parapodium 100; (e) heterogomph falciger, parapodium 20, neuropodium, subacicular fascicle.

**Distribution.** Australia (north-west Australia from 17°58'S 122°13'E, Broome, WA to 27°21'S 153°07'E, Cribb Island, Qld). Also from China, India, Andaman Islands, Indonesia (Sulawesi, Sumatra, Java), Philippines*.

### *Perinereis amblyodonta* (Schmarda)

Fig.3a-h

*Nereilepas amblyodonta* Schmarda, 1861: 106, fig.A-B, a-b, K, pl.31, fig.245.

*Perinereis novaehollandiae* Kinberg, 1866: 175.–Augener, 1924: 342-348.–Augener, 1927: 347.–Pope, 1943: 238, 244.–Knox, 1951: 213, 218, 221-222, pl.48, figs 25-31.

*Nereis amblyodonta*.–Ehlers, 1904: 28-29.–Ehlers, 1907: 11.

*Perinereis amblyodonta*.–Augener, 1913: 174-175.–Monro, 1926: 320.–Kott, 1951: 113, fig.6e-g.–Hartman, 1954: 18, 33-34, charts I-IV.–Knox, 1960: 122.–Knox & Cameron, 1971: 28.–Hutchings & Turvey, 1982: 139.–Hartmann-Schröder, 1987: 48.

**Material examined.** Australia: Queensland – Shute

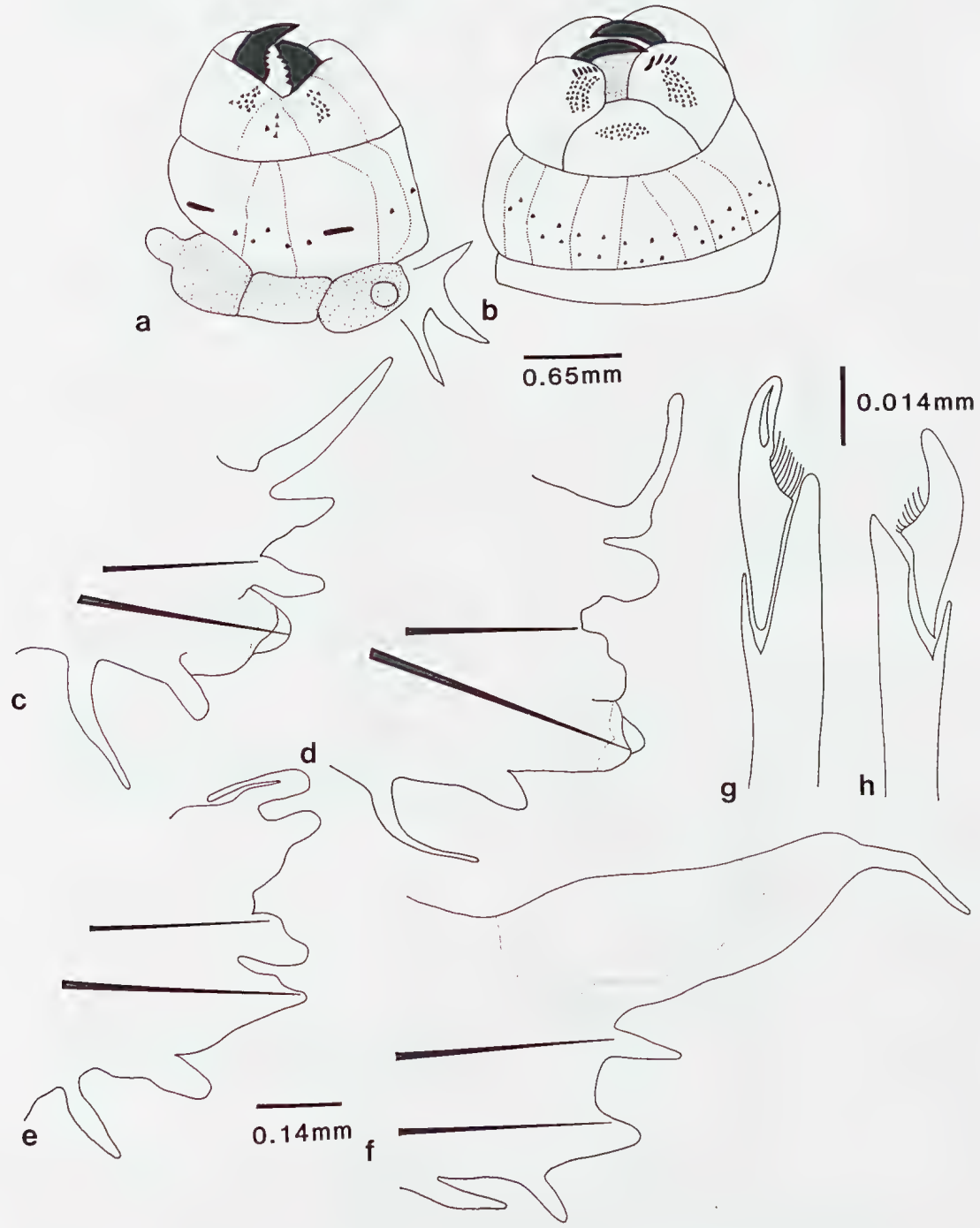


**Fig.3.** *Perinereis amblyodonta* AM W4859. (a) everted pharynx dorsal view; (b) everted pharynx ventral view; (c) parapodium 3; (d) parapodium 10; (e) parapodium 25; (f) parapodium 72; (g) heterogomph falciger, parapodium 10, neuropodium, subacicular fascicle; (h) heterogomph falciger, parapodium 72, neuropodium, subacicular fascicle.

Harbour, 20°18'S 148°47'E, 27 Sept. 1970, several (AM W4920); Pialba, Hervey Bay, 25°17'S 152°50'E, 30 Mar. 1972, 2 (AM W202787); Caloundra, 26°48'S 153°08'E, 29 Mar. 1972, 2 (AM W202543); Myora, 27°29'S 153°25'E, 19 Dec. 1950, 1 (QM G4090). New South Wales – Lennox Head, 28°48'S 153°36'E, 27 Mar. 1972, 3 (AM W202798); Minnie Waters, 29°47'S 156°16'E, 27 Feb. 1971, 1 (AM W202797), 25 Sept. 1982, 1 (W198490); Coffs Harbour, 30°18'S 153°08'E, July 1976, 3 (AM W203040); Nambucca Heads, 30°39'S 153°01'E, Nov. 1974, 2 (AM W202802); Harbord, 33°47'S 151°17'E, 2 (AM W4858), 29 July 1964, 20 (W202789); Port Jackson, 33°53'S 151°15'E, many (AM W4859), 5 (W202604); Wreck Bay, 35°11'S 150°38'E, 27 Feb. 1976, 6 (AM W202785); Twofold Bay, 37°05'S 149°54'E, 2 (AM W202786); Twofold Bay, Munganno Point, 37°06'S 149°56'E, 1 (AM W202805). Victoria – Mallacoota, Bastion Point, 37°34'S 149°46'E, 1 (AM W202807); Wilsons Promontory, 38°56'S 146°22'E, Jan. 1978, 12 (AM W202791); Lorne, 38°32'S 143°58'E, 27 Mar. 1975, 1 (AM W202811). Tasmania – Flinders Island, Lady Barron, 40°13'S 148°15'E, 10 Apr. 1977, 3 (AM W202821); Darlington, Maria Island, 42°35'S 148°04'E, 14 Apr. 1968, 1 (TASM K997); Flinders Island, 40°01'S 148°02'E, 1 (AM W202822); Eaglehawk Neck, 43°01'S 147°55'E, Mar. 1941, 1 (TASM K996); Dunalley, 42°53'S 147°49'E, 30 June 1965, 6 (TASM K165); Bellerive, 42°52'S 147°22'E, Jan. 1939, 1 (TASM K993); Bicheno, 41°53'S 147°18'E, 6 Feb. 1965, many (AM W4820). South Australia – Beachport, 37°29'S 140°00'E, 9 Feb. 1977, 1 (SAM E2347); Karatta, 35°59'S 136°56'E, 28 Feb. 1978, 2 (AM W202792); Lusby Island, 34°33'S 136°16'E, 27 Feb. 1975, 1 (SAM E2349); Baird Bay, 33°07'S 134°20'E, 29 Jan. 1985, 1 (SAM E2348); Pearson Island, 33°58'S 134°17'E, 24 Nov. 1976, 5 (SAM E2350). Western Australia – Garden Island, 32°12'S 115°40'E, 1950, several (WAM 475-86); Fremantle, 32°03'S 115°44'E, 22 June 1979, 1 (AM W202808); Cape Peron, 25°30'S 113°31'E, 22 Feb. 1952, several (WAM 537-86); Kendrew Island, 20°29'S 116°32'E, 18 May 1973, several (WAM 47-74).

**Description.** Material examined up to 35 mm length, 1.5-4.0 mm width, 0.9-3.2 mm jaw length. Colour in alcohol green, cream-pink with olive pigmentation on dorsum of anterior and far posterior setigers. Live colouration olive green. Prostomium as broad as long, rectangular, deeply indented anteriorly, eyes with distinct lenses. Robust palps with globular palpostyles, antennae broad based. Tentacular cirri, faintly annulated, longest extending to setiger 4. Jaws robust, heavily sclerotised. Pharynx with conical paragnaths on both rings and smooth bars on Areas VI and IV arranged as follows: I=2-5 (usually 2), II=11-28 in an irregular triangular patch, III=14-36 in an ovoid patch, sometimes with 1-2 cones separate and lateral to main group of cones, IV=a rectangular patch of 18-63 cones in 3-8 rows, 2-4 bars on dorsal-most edge (closest to Area II), V=1-3, VI=1 bar, 2-3 cones, VII-VIII=33-50 in 2 irregular rows (Figs 3a,b).

Anterior notopodia with dome-shaped notopodial and median ligules of equal length, superior lobes present. Dorsal cirrus greatly exceeding parapodial lobes in length. Neuropodia with digitiform superior lobes, dome-shaped inferior lobes and shorter, scalloped postsetal lobes. Ventral ligules also dome-shaped (Figs 3c-e). Ventral cirrus slightly shorter than ventral ligule. Median and posterior parapodia, dorsal ligule greatly elongate, strap-like, flattened, with dorsal cirrus emerging from distal tip as a finger-like extension (Fig.3f). Remaining lobes as for anterior setigers with shape tending to subtriangular rather than dome-shaped. Ventral ligule reduced in size in far posterior setigers.

Neurosetae with homogomph spinigers and heterogomph falcigers in the supra-acicular fascicle, heterogomph falcigers in the subacicular fascicle (Figs 3g,h). Anal cirri very long, slender.

**Remarks.** Type material of *Perinereis novaehollandiae* (from Port Jackson, NSW) was redescribed by Augener (1922c). Descriptions of other authors (e.g., Hartman, 1954; Hutchings & Turvey, 1982) are in agreement, and the above description is provided for the sake of completeness. The arrangement of cones in the dorsalmost position of the oral ring is typically a central cone towards the maxillary end with a transverse line of four cones arranged behind. These are usually recorded as occurring on Area V, however the cones comprising the transverse row often lie completely or partially on Area VI. An additional cone is often seen in line with these in a position ventral to the single smooth bar on Area VI. *Perinereis amblyodonta* often occurs with *P. barbara* Monro, 1926, and care must be taken to distinguish the two species which can be separated on the basis of the shape of the dorsal notopodial ligules on posterior segments and the numbers of paragnaths on Areas III and VII-VIII (see couplet 3 of the key).

**Habitat.** Occurs intertidally, under rocks, among barnacles, mussel beds, weed and clumps of the serpulid *Galeolaria*. Also found among algal holdfasts and coralline algae.

**Distribution.** Australia (southern Australia, from 20°18'S 148°47'E, Shute Harbour, Qld to 17°46'S 122°12'E, Broome, WA). Also from New Zealand and the Philippines.

### *Perinereis barbara* (Monro)

Fig.4a-g

*Nereis* (*Perinereis*) *barbara* Monro, 1926: 316-317, figs 3-5.
*Perinereis barbara*.–Fauvel, 1953: 204, fig.103d-f.–Hutchings & Murray, 1984: 41-42.

**Material examined.** Australia: Queensland – Maroochydore, 26°39'S 153°06'E, 1 (AM W202544); Caloundra, 26°48'S 153°08'E, 29 Mar. 1972, 2 (AM W202543). New South Wales – Lennox Head, 28°48'S 153°36'E, 27 Mar. 1972, 2 (AM W202542); Angourie Point, 29°21'S 153°22'E, 1 (AM W202539); Minnie Water, 29°47'S 156°16'E, 1 (AM W202548); Coffs Harbour, 30°18'S 153°08'E, 25 Mar. 1972, 1 (AM W202535), 3 (AM W202537), 10+ (AM W202541); Broken Bay, Box Head, 33°33'S 151°21'E, 11 Apr. 1981,

many (AM W19353), 1 (AM W19355), 2 (AM W19356); Collaroy, 33°44'S 151°18'E, 1 (AM W4425); Long Reef, 33°45'S 151°19'E, Feb. 1940, 3 (AM W3227), 22 Sept. 1968, 3 (AM W4494), 23 Feb. 1971, 11 (AM W4839); Manly, 33°48'S 151°17'E, 20 Dec. 1968, 2 (AM W4320); Port Jackson, 33°49'S 151°18'E, 8 SYNTYPES (BM ZK1926.4.30.107.112), (BM ZK1926.4.30.129); Mosman, Spit Bridge, 33°50'S 151°15'E, 29 Mar. 1972, 2 (AM W202547); Coogee Bay, 33°56'S 151°16'E, Dec. 1921, 17 (AM W4795); La Perouse, 33°59'S 151°15'E, 24 Oct. 1962, 7 (AM W4788); Cape Solander, Kurnell Peninsula, 34°00'S 151°13'E, 12 July 1988, 2 (AM W202819); Port Hacking, 34°05'S 151°10'E, 1 (AM G11263), 6 Feb. 1962, 19 (AM W4792); Bellambie Beach, 34°22'S 150°56'E, 14 Nov. 1971, 1 (AM W202545); Wreck Bay, 35°11'S 150°38'E, 27 Feb. 1976, 2 (AM W202540); Moruya Heads, 35°55'S 150°10'E, 23 May 1960, 1 (AM W4797); Bermagui, 36°25'S 150°04'E, 25 May 1960, 2 (AM W4798); Twofold Bay, Munganno Point, 37°06'S 149°56'E,

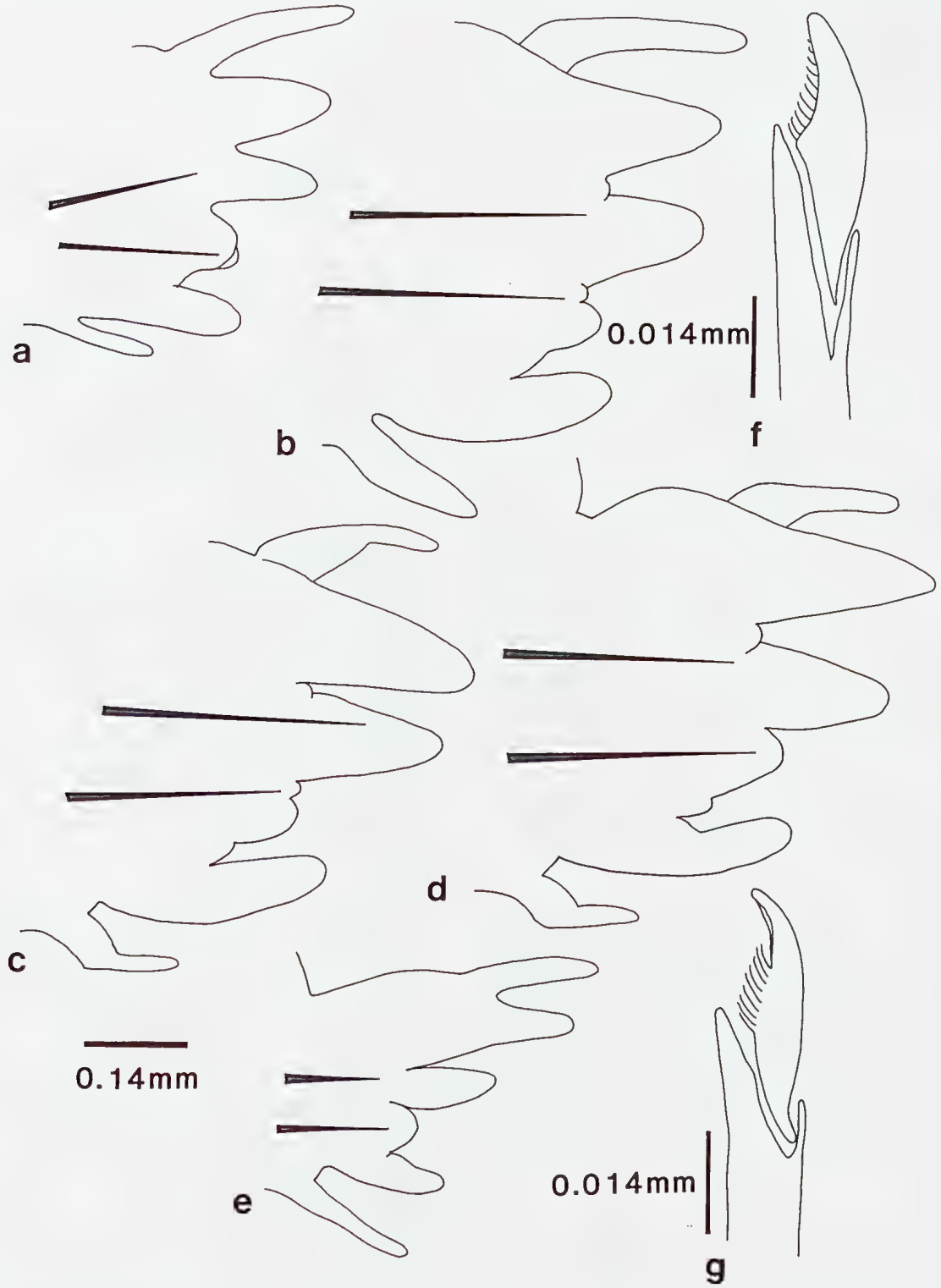


**Fig.4.** *Perinereis barbara* SYNTYPE BM ZK 1926.4.30.129. (a) parapodium 3; (b) parapodium 10; (c) parapodium 25; (d) parapodia 50; (e) parapodium 80; (f) heterogomph falciger, parapodium 10, neuropodium, subacicular fascicle; (g) heterogomph falciger, parapodium 50, neuropodium, supra-acicular fascicle.

1 (AM W202546). Victoria – Bastion Point, 37°34'S 149°46'E, 1 (AM W202536); Separation Creek, 38°37'S 143°53'E, 27 Oct. 1985, 3 (NMV F56467). South Australia – Murray River mouth, 35°34'S 138°53'E, 31 Dec. 1971, 3 (AM W203022).

**Description.** Material examined up to 40 mm length, 1.0-4.5 mm width, 1-3.6 mm jaw length. Colour in alcohol, cream-coffee coloured, some specimens with faint pigmentation on prostomium and anterior setigers. Prostomium longer than broad, ovoid anteriorly, eyes large with distinct lenses. Palps large, globular, with elongate palpostyles. Antennae bluntly pointed, triangular, set closely together. Longest tentacular cirri extending to setiger 3. Jaws robust with approximately 7 teeth. Pharynx with conical paragnaths on both rings and smooth bars present on Areas IV and VI arranged as follows: I=0-3 (usually 1-2), II=6-14 in 2 curved rows, III=3-7, IV=9-23 plus 2-3 bars, V=2-7, VI=1 bar plus 1-5 cones (usually 2-3), VII-VIII=45-101 in 2-4 irregular rows.

Notopodial ligules cylindrical in far anterior setigers and of equal length (Figs 4a,b). After first few setigers, dorsal notopodial ligule very robust, dome-shaped and slightly exceeds length of median ligule (Fig.4c). Superior lobes short digitiform and closely abutting median ligule. Neuropodia with digitiform superior lobe, larger digitiform inferior lobe, postsetal lobe low, with scalloped border. Superior lobes positioned posterior to inferior lobes. Ventral ligule conical, similar to median ligule in size and shape. Ventral cirrus slightly shorter than ventral ligule. Aciculum tip projects slightly. Dorsal notopodial ligule gradually becoming subtriangular (Fig.4d), greatly expanded and very broad basally and curved dorsally on median and posterior parapodia. Dorsal cirri becoming more distally inserted on dorsal notopodial lobe on posterior setigers (Fig.4e). Superior neuropodial lobe reduced on median and posterior setigers.

Neurosetae with homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph falcigers in subacicular fascicle (Fig.4f,g). Anal cirri relatively short.

**Remarks.** *Perinereis barbara* may be confused with *P. amblyodonta* Schmarda, 1861, with which it often occurs. Distinguishing characters of the two species are given in the Remarks section of *P. amblyodonta*. Male epitokous specimens collected from Long Reef, Sydney in September 1968 (AM W4494) and Kurnell, New South Wales in July 1988 (AM W202819) showed modification of parapodia from setiger 14. A female epitoke (AM W4494) was modified from setiger 20 onwards. In life the colour of epitokes is red-dark green.

**Habitat.** Occurs intertidally, often among the ascidian *Pyura*, algal holdfasts, calcareous algae, or in rock crevices and under boulders.

**Distribution.** Australia (eastern Australia, from 26°39'S 153°06'E, Maroochydore, Qld to 35°34'S 138°53'E, Murray River mouth, SA). Also from India and Singapore.

### *Perinereis calmani* (Monro)

Fig.5a-e

*Nereis* (*Perinereis*) *calmani* Monro, 1926: 318-320, figs. 6-8.
*Perinereis calmani*.–Hartman, 1954: 18.–Russell, 1962: 7.

**Material examined.** Australia: Queensland – Point Vernon 25°15'S 152°49'E, 23 Oct. 1976, 1 (AM W202522), Mar. 1972, 1 (AM W202523), 31 Apr. 1972, 4 (AM W202524), Apr. 1972, 7 (AM W202525); Dunwich 27°30'S 153°24'E, 20 Dec. 1950, 2 (QM G4089), 29 Mar. 1952, 1 (QM G4012). New South Wales – Arrawarra, 30°04'S 153°12'E, 21 Mar. 1978, 2 (AM W202526); South Solitary Island, 30°12'S 153°16'E, 18 May 1972, 4 (AM W202527); Fairlight, 33°48'S, 151°17'E, 23 Oct. 1976, 1 (AM W20252); Port Jackson, 33°49'S 151°18'E, SYNTYPES, 2 (BM ZK1926.4.30.80-81), 4 (BM ZK1926.4.30.92-95); Port Jackson 33°49'S 151°18'E, several (AM W4828); North Head, 33°50'S 151°18'E, 26 Mar. 1972, 1 (AM W6876); Green Patch, Jervis Bay, 34°39'S 135°47'E, 23 Jan. 1973, 1 (AM W202529).

**Description.** Material examined 11-52 mm length, 1-3 mm width, 0.85-2.8 mm in jaw length, up to 80 setigers. Colour in alcohol yellow-cream, sometimes with mid-dorsal, longitudinal brown pigmentation band. Prostomium about as long as wide, with shallow mid-dorsal depression anteriorly. Eyes large, palps cylindrical, widely spaced, with bluntly globular palpostyles, antennae short, cylindrical. Tentacular cirri annulated, dorsalmost longest, extending to setiger 2. Peristomium relatively long. Jaws robust, heavily sclerotised with 3-4 large teeth. Pharynx with conical paragnaths on both rings and smooth bars on Area VI arranged as follows: I=1-3, II=8-32 in 2-4 curved rows, III=7-13 in 2-3 rows, IV=9-26 in a triangular patch, V=0; VI=1 short bar, VII-VIII=10-13 in 2 irregular rows. Area IV without bars.

Anterior notopodia with short, conical notopodial ligules, slightly longer, conical median ligules, superior lobes short, digitiform, closely apposed and slightly anterior to median ligule, dorsal cirrus relatively short, approximately equal in length to dorsal ligule (Figs 5a,b). Notopodial ligules exceed length of neuropodial ligules throughout. Neuropodia with digitiform superior and conical bluntly-rounded inferior lobes and single, slightly curved postsetal lobe. Superior lobes positioned posterior to inferior lobes. Acicular and postsetal lobes subequal. Ventral cirri as long as ventral neuropodial ligule in anteriormost setigers, reducing to approximately two thirds as long as ventral ligule posteriorly. Median and posterior notopodia similar, however notopodial ligules conical anteriorly, becoming subtriangular posteriorly (Figs 5c,d). Dorsal cirri gradually becoming more distally inserted on dorsal notopodial ligule on posterior setigers. Dorsal notopodial ligule increasing

in size posteriorly, becoming longer than median ligule. Dorsal notopodial lobe becoming very broad and basally glandular in far posterior setigers, but not greatly expanded in length. Neuropodial ligules reduced to short lobe. Neuroaciculae slightly emergent.

Neurosetae with homogomph spinigers and heterogomph falcigers (Fig.5e) in supra-acicular fascicle, heterogomph falcigers and single heterogomph spiniger in subacicular fascicle. Anal cirri long, tapering.

**Remarks.** A band of dorsal pigmentation may be present or absent. The specimens from Dunwich (QM G4089) are dark brown in colour, and agrees well with previously published descriptions and with the type material.

**Habitat.** Intertidal among and under rocks, kelp holdfasts and sponges. Often occurs among tubes of the serpulid *Galeolaria* and barnacles.

**Distribution.** Australia (eastern Australia, from 25°15'S 152°49'E, Point Vernon, Qld to 34°39'S 135°47'E, Jervis Bay, NSW). Also from China.

**Fig.5.** *Perinereis calmani* SYNTYPE BM ZK 1926.4.30.92.95. (a) parapodium 3; (b) parapodium 10; (c) parapodium 25; (d) parapodium 50; (e) heterogomph falciger, neuropodium, supra-acicular fascicle.

### *Perinereis camiguinoides* Augener

Fig.6a-c

*Nereis* (*Perinereis*) *camiguinoides* Augener, 1922b: 180-183, fig.4a-d, tafelfig. 2.

**Material examined.** Chile: Juan Fernandez Islands, 34°S 80°W, coll. Plate, 2 SYNTYPES (ZMB 5645).

**Description.** Entire specimens, both 58 setigers, 24 mm length, 1.1(1.6)-2.0(3.1) mm width. Jaw length 11-18 mm. Eyes black. Prostomium as long as wide. Antennae half as long as prostomium, longest tentacular cirri extend back 3-5 setigers. Jaws with 3-6 lateral teeth. Paragnaths: I=1 large cone; II=6-7; III=5-6 (no lateral groups); IV=13-17 cones, 1-2 bars in one specimen, bars absent in remaining specimen; V=3; VI=2 bars (broken on one specimen, giving appearance of 3 bars on one side); VII-VIII=43-50 in 2 irregular rows. Notopodia anteriorly with 2 equal lobes and short, conical superior lobe, dorsal ligule 2 times ventral ligule on posteriormost 20 setigers. Dorsal cirrus 1.25 times length of dorsal notopodial ligule. Neuropodia with 2 equal lobes throughout, equal to length of notopodia. Ventral cirrus as long as neuropodia (Fig. 6a,b). Anal cirri extend back 3-5 setigers. Neurosetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph spinigers and falcigers (Fig.6c) in subacicular fascicle (heterogomph spinigers present from setiger 1).

**Remarks.** We have provided the above redescription because the original (Augener, 1922b) omits some information that we consider to be of taxonomic value: presence/absence of lateral groups on Area III and of bars on Area IV, and presence of heterogomph spinigers in early parapodia.

**Habitat.** Unknown.

**Distribution.** Chile (Juan Fernandez Islands*). Also recorded from New Zealand (Augener, 1924, 1927; Ehlers, 1904).

### *Perinereis cavifrons* Ehlers

Fig.7a-c

*Nereis* (*Perinereis*) *cavifrons* Ehlers, 1920: 47-49, pl.1 figs 6-10.

**Material examined.** Indonesia: Java – Nordwachter Eiland, no further data, coll. Brock, HOLOTYPE (ZMB 6740).

**Description.** Holotype an entire epitoke, 138 setigers, about 60 mm length, 2.5 (5.0) mm width. Jaw length 32 mm. Eyes black. Prostomium three quarters as long as wide, with deep longitudinal median groove on anterior half. Antennae third as long as prostomium, longest tentacular cirri extend back 5 setigers. Jaws with 3-4 lateral teeth. Paragnaths: I=2 large cones; II=8,11; III unknown (damaged); IV=at least 17 cones, no bars (damaged); V=3 large cones in a triangle; VI=1 curved bar; VII-VIII=16 in 1-2 irregular rows. Notopodia anteriorly with 2 lobes, dorsal ligule 1.25 times median ligule. Dorsal cirrus 1.25 times length of dorsal notopodial ligule. Neuropodia with 2 equal lobes equal to length of notopodia. Ventral cirrus three quarters as long as ventral ligule (Fig.7a). Anal cirri extend back

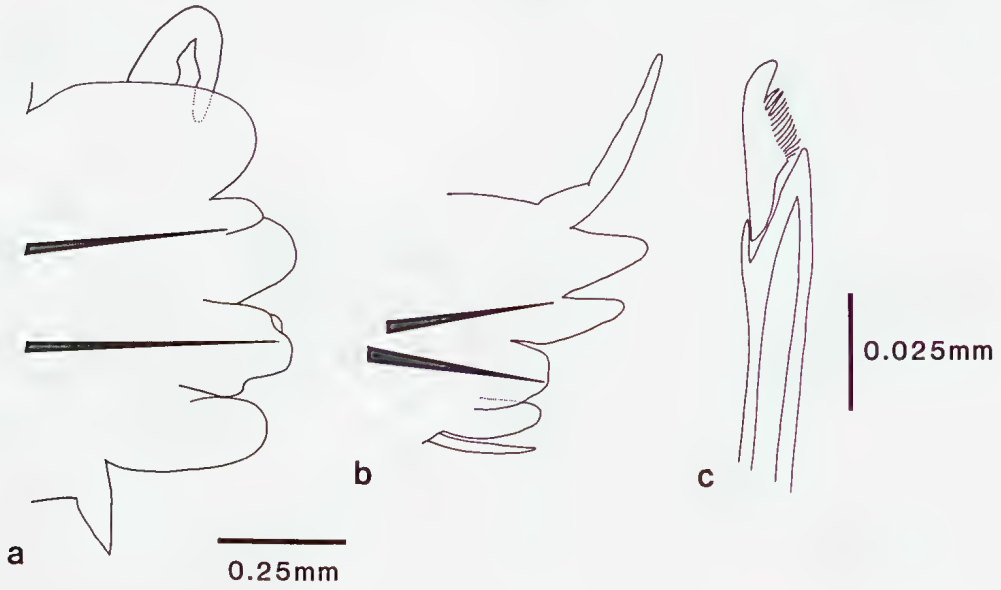


**Fig.6.** *Perinereis camiguinoides* SYNTYPE ZMB 5645. (a) parapodium 12; (b) parapodium 51; (c) heterogomph falciger, parapodium 12, neuropodium, subacicular fascicle.

4 setigers. Base of dorsal cirri inflated on setigers 1-4, ventral cirri inflated setigers 1-3. Epitokal modifications present from setiger 20 (Fig.7b). Many anterior setae broken, but heterogomph spinigers present from setiger 2 at least. Heterogomph falcigers (Fig.7c) similar to *P. cultrifera* (Grube, 1840) and *P. helleri* Grube, 1878, but have longer blades than those of most other species of *Perinereis*.

**Remarks.** Fauvel (1932) recorded two atokous specimens of *P. cavifrons* from India, and noted that the posterior parapodia were not modified (i.e., dorsal notopodial lobes not expanded). Fauvel's description is, however, too brief to be sure that his material is conspecific with the holotype. The poor condition of the pharynx of the holotype, and the lack of atokous type material will make it difficult to identify any future specimens as *P. cavifrons*.

**Habitat.** Unknown.

**Distribution.** Recorded only from Indonesia (Java*).

***Perinereis cultrifera*** (Grube)

Fig.8a-c

*Nereis cultrifera* Grube, 1840: 74, fig.6.

**Material examined.** Mediterranean Sea: Naples, 40°51'N 14°17'E, 19 probable syntypes, ZMB 5653, [label reads "Neapel", no further data].

**Description.** Entire specimens and anterior fragments, all close to 111 setigers, 85 mm length, 4.5(5.5) mm width. Jaw length 18-30 mm. Faint narrow transverse pigmented bands on several anterior setigers, otherwise lacking pigmentation patterns. Prostomium four fifths as long as wide, eyes black. Antennae one third as long as prostomium, longest tentacular cirri extend back 4-5 setigers. Jaws with about 7 distinct teeth. Paragnaths: I=1-2; II=3-15, usually 5-9; III=5-11, lateral groups present in about half of all specimens; IV=6-20 cones, usually 10-15, no bars; V=2-5, usually 3-4; VI=1; VII-VIII=20-50, usually 30-40. Notopodia with 2 equal lobes anteriorly, and superior lobe on setigers 3-35. Dorsal cirrus as long as dorsal notopodial ligule anteriorly (Fig.8a). Dorsal notopodial ligule expanded up to 2 times length of median ligule on posteriormost 20-30 setigers (Fig.8b), but not greatly expanded. Neuropodia with 2 equal lobes throughout, three quarters as long as median notopodial ligule. Ventral cirrus three quarters length of neuropodium. Heterogomph spinigers present in ventral neuropodial fascicles from setiger 1. Heterogomph falcigers (Fig.8c) similar to *P. cavifrons* Ehlers, 1920 and *P. helleri* Grube, 1878, but have longer blades than those of most other species of *Perinereis*. Anal cirri extend back about 7 setigers.

**Remarks.** *Perinereis cultrifera* has been reported from most temperate oceans. Taxonomic confusion in *P. cultrifera* dates from the work of Fauvel (1932), who introduced several varieties or subspecies into the literature. Fauvel's own comments show that the supposed varieties do not designate geographically distinct populations and should not be considered of taxonomic significance. ("They are not even local races ... most are found wherever *P. cultrifera* is plentiful ... intermediate forms are frequent ..." Fauvel, 1932: 104.) Among the species synonymised with *P. cultrifera* by Fauvel (1932) are: *Nereis* (*Perinereis*) *floridana* Ehlers, 1868, *Nereis* (*Perinereis*) *perspicillata* Grube, 1878, *Nereis* (*Perinereis*) *striolata* Grube, 1878, *Nereis* (*Perinereis*)

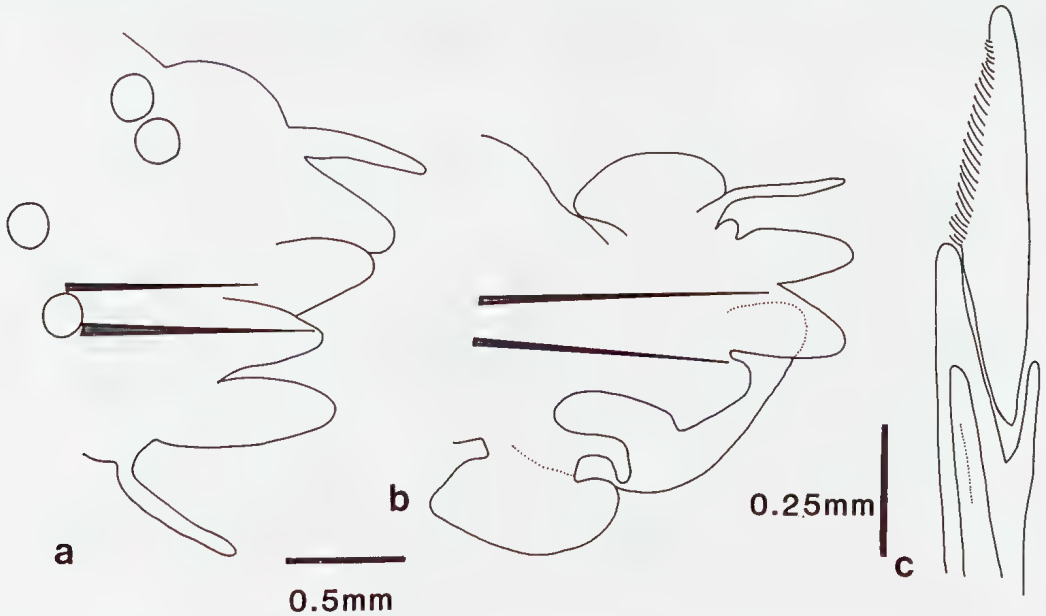


**Fig.7.** *Perinereis cavifrons* HOLOTYPE ZMB 6740. (a) parapodium 13; (b) parapodium 40; (c) heterogomph falciger, parapodium 13, neuropodium, subacicular fascicle.

*helleri* Grube, 1878, and *Nereis* (*Perinereis*) *obfuscata* Grube, 1878. *Perinereis hedenborgi* Kinberg, 1866 was synonymised with *P. cultrifera* by Hartman (1948). In this paper we have retained *P. helleri* Grube as a distinct species (see below), but have been unable to re-evaluate all records of *P. cultrifera*. Full revision of this group will require large samples of specimens from throughout the nominal range of the species. Additional distributional records that require verification include Marshall Islands (Reish, 1968), New Caledonia (Rullier, 1972), India (Fauvel, 1932), South Africa and Madagascar (Day, 1967), Japan (Izuka, 1912; Imajima, 1972).

*Perinereis cultrifera* is a widely used experimental animal in physiological and biochemical studies. In view of the current taxonomic confusion, all workers should include the provenance of experimental material used in all publications.

**Habitat.** Intertidal.

**Distribution.** Mediterranean Sea*, English Channel; more widespread records require verification.

### *Perinereis helleri* (Grube)

Fig.9a-c

*Nereis Perinereis helleri* Grube, 1878: 81-82.–Horst, 1924: 172-173, pl.34, figs 3, 4.
*Perinereis helleri* Monro, 1931a: 14-15, fig.8a-c.–Russell, 1962: 7.–Rozbaczylo & Castilla, 1973: 220-221.–Hartmann Schröder, 1979: 116.
*Perinereis cultrifera* var. *helleri* Fauvel 1932: 105-106.
*Perinereis camiguina* Grube, 1878: 87, pl.4 fig.8.

**Material examined.** Philippines: Bohol Island 10°S 124'E, HOLOTYPE or SYNTYPE, *Nereis* (*Perinereis*) *helleri*, (WMNH, 310); Camiguin, 9°11'N 124°42'E, coll. Semper, 2 SYNTYPES *Perinereis camiguina* (ZMB Q3464).

Australia: Western Australia – Enderby Island, 20°36'S 116°30'E, 2 Apr. 1987, 4 (AM W203048); Kendrew Island, 20°29'S 116°32'E, 2 May 1973, 1 (WAM 179-86); Broome, 17°58'S 122°13'E, 2 Oct. 1982, 2 (NTM W2319), 30 Sept. 1984, 1 (NTM W2153), 2 Oct. 1984, 1 (NTM W2192), 1 (NTM W2201), 1 (NTM W2306), 1 (NTM W2318), 1 (NTM W2320); Rat Island, 16°24'S 123°07'E, 5 May 1974, 2 (WAM 479-86); Albert Island, 14°31'S 124°55'E, 14 July 1988, 1 (AM W202977); Descartes Island, 14°11'S 125°04'E, 20 July 1988, 2 (AM W202988), 1 (AM W202989); Corneille Island, 14°12'S 125°44'E, 19 July 1988, 2 (AM W202984), 1 (AM W202985), 2 (AM W202987); Careening Bay, 15°06'S 125°06'E, July 1988, 1 (AM W203091); Coronation Island, 15°05'S 124°56'E, 13 July 1988, 3 (AM W202998); Port Keats, 14°06'S 129°33'E, 23 July 1952, 2 (AM W202532); Burford Island, 11°29'S 131°57'E, 13 Oct. 1981, 1 (NTM W13); Port Essington, 11°16'S 132°09'E, 17 May 1985, 10 (NTM W403); Port Bremner, Danger Point, 11°07'S 132°20'E, 30 Apr. 1982, 2 (NTM W214); Oxley Island, 10°59'S 132°50'E, 20 Oct. 1982, 1 (NTM W420), 1 (NTM W421), 22 Oct. 1982, 1 (NTM W423); Annesley Point, 11°24'S 132°51'E, June 1984 (NTM W1772), 16 June 1984 (NTM W1806), 19 June 1974, 2 (NTM W2062); New Year Island, 10°55'S 133°01'E, 18 Oct. 1982 (NTM W412). Queensland – Torres Strait, Prince of Wales Island, 10°41'S 142°09'E, 29 May 1969, 1 (NMV 56466); Thursday Island, 10°35'S 142°13'E, 4 (AM W4842), Sept. 1908, 1 (AM G11246), 29 June 1976, 1 (AM W202533); Lizard Island, 14°40'S 145°28'E, 10 Dec. 1987, 1 (AM W203038), 1 (AM W203039); Low Islets, 16°23'S 145°34'E, Jan. 1917, 10+ (AM W418), Oct. 1931, 1 (AM W2928); Saxon Reef, 16°28'S 145°59'E, 4 May 1971, 1 (AM W202820); Cairns, Michaelmas Reef, 16°35'S 146°02'E, 8 Apr. 1979, 1 (AM W203049); Cairns, 16°55'S 145°46'E, 1 (AM W2356), 1 (AM W2383); Townsville, 19°16'S 146°49'E, 4 Aug. 1981, 1 (AM W202534); Shute Harbour, 20°18'S 148°47'E, 27 Sept. 1970, 1 (AM W4920); Port Molle, 20°20'S 148°51'E, 1 (AM W4829); Heron Island, 23°27'S 151°55'E, 1961, 4 (AM W197105); Gladstone, 23°51'S 151°16'E, 15 Aug. 1951, 1 (QM GH4000); Gladstone, Calliope River, 23°55'S 151°10'E, 1 (AM W199384); Dunwich, 27°30'S 153°24'E, 18 Mar. 1961, 1 (QM G7130). New South Wales – Lord Howe Island, 31°33'S 159°05'E, Nov. 1983, 1 (AM W198421), Nov. 1983, 1 (AM W198422), 1 (AM W198423).

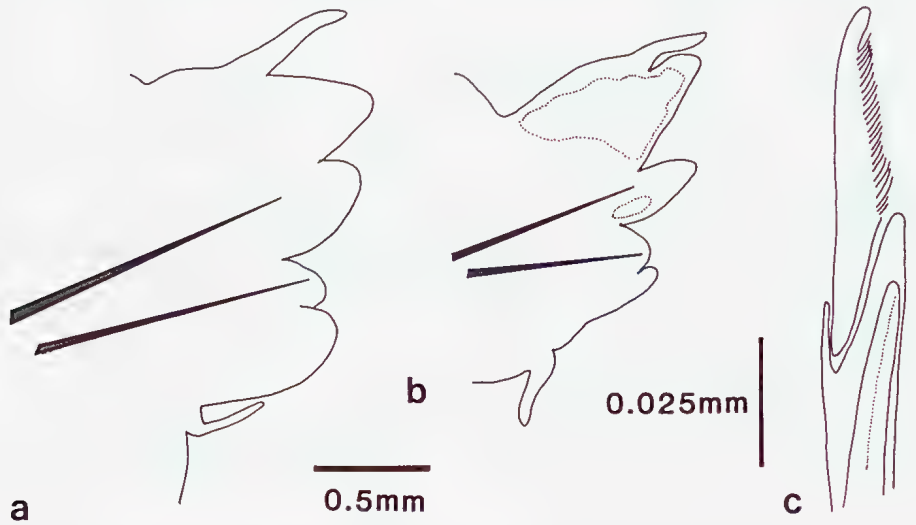


**Fig.8.** *Perinereis cultrifera* SYNTYPE ZMB 5653. (a) parapodium 15; (b) parapodium 90; (c) heterogomph falciger, parapodium 15, neuropodium, subacicular fascicle.

**Description.** Material examined up to 75 mm length, 3.5 mm width, 1.0-2.7 mm in jaw length, 155 setigers maximum. Colour in alcohol cream-pink or light brown. Prostomium with deep median furrow. Palps with large dome-shaped, cylindrical palpophores, globular palpostyles. Antennae triangular. Longest tentacular cirri extending to setiger 16 (range 8-16). Peristomium relatively short. Jaws robust, heavily sclerotised with about 8 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Areas VI, arranged as follows: I=2 (occasionally 1); II=4-17, III=11-20 in ovoid-rectangular patch with 2-3 cones displaced laterally, separate from main group, IV=10-19 (1 specimen with 4), V=3; VI=1 long straight bar, VII-VIII=21-40 in 2 rows. Area IV without bars.

Anterior notopodia with subtriangular notopodial ligules, equal to or slightly longer than median ligules (Fig.9a); superior lobes present. Dorsal cirri longer than dorsal ligule on all setigers. Neuropodia with superior lobe not visible, crescent-shaped inferior lobe and slightly shorter postsetal lobe with digitiform projection where aciculum emerges. Ventral ligule sub-triangular, ventral cirrus slightly shorter than ventral ligule. Dorsal notopodial ligule longer than median ligule in far posterior setigers but only slightly enlarged. Ventral ligule reduced posteriorly (Fig.9b). Ventral cirrus longer than ventral neuropodial ligule.

Neurosetae with homogomph spinigers and heterogomph falcigers (Fig.9c) in supra-acicular fascicle; heterogomph spinigers and falcigers in subacicular fascicle. Anal cirrus extend back about 9-10 setigers.

**Remarks.** We follow Fauvel (1932) in synonymising *Perinereis camiguina* Grube, 1878 with *P. helleri*. A number of epitokous specimens were collected by torchlight and dipnet in November and December of 1985 to 1987 at Lizard Island, Queensland. Two male specimens (AM W203038) were modified from setiger 19 onwards, a female (AM W203039) showed modification from setiger 21 onwards. Russell (1962) also reports the collection of epitokous specimens from Heron Island, Queensland.

*Perinereis helleri* was described as *P. cultrifera* var. *helleri* by Fauvel, 1932. Fauvel describes *P. cultrifera* as 'a species liable to extensive variation, especially as regards the armature of the pharynx, length of the dorsal cirri and the shape of the dorsal ligule', and his 1932 paper provides a key to six varieties of *P. cultrifera*. The Australian material described here is consistent with the syntypes of *Perinereis helleri*, and differs from the probable syntypes of *Perinereis cultrifera* from the Mediterranean Sea in paragnath counts for Area III (see description of *P. cultrifera* above). *Perinereis helleri* has 11 to 20 paragnaths on Area III, whereas *P. cultrifera* has 4 to 11. We therefore prefer to retain *P. helleri* as a distinct species pending a full revision of *P. cultrifera* and similar species on a worldwide basis.

The length of the dorsal cirri is very variable but always exceeds length of the notopodial ligule. Fauvel (1932) used this character to distinguish *P. helleri* from other taxa in the *P. cultrifera* complex, but our observations suggest that this character is too variable to be useful in this group. The heterogomph falcigers of *P. helleri* are similar to *P. cavifrons* Ehlers, 1920 and *P. cultrifera*, but have longer blades than those present in most other species of *Perinereis*.

The number and arrangement of paragnaths appears to be very consistent within the material examined from a wide range of localities.

**Habitat.** Occurs among coral rubble and sand, and on reef flats.

**Distribution.** Australia (northern, north-western and eastern Australia from 20°36'S 116°30'E, Enderby Island, Western Australia to 33°52'S 124°66'E, New Year Island, New South Wales). Also from the Philippines*, Indonesia, Ambon Reef, India, Chile.

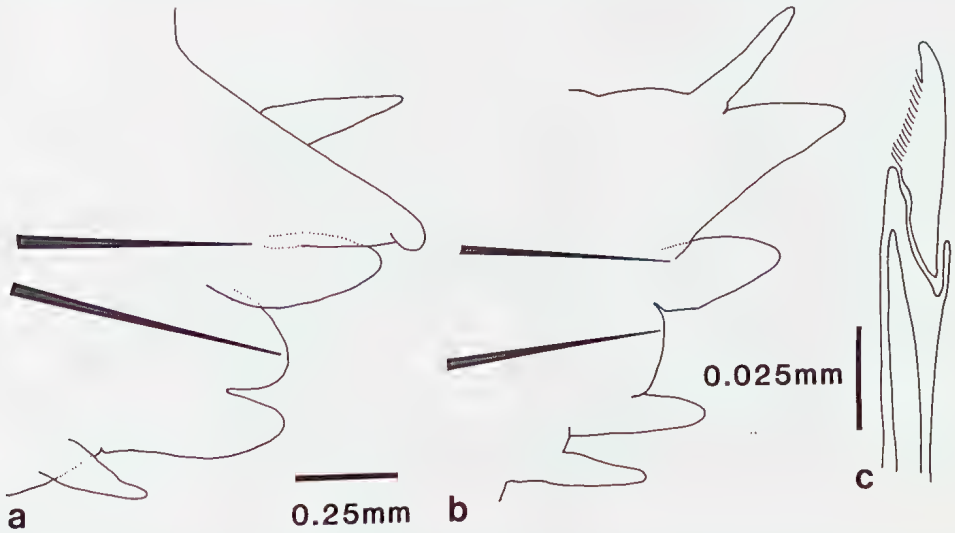


**Fig.9.** *Perinereis helleri* SYNTYPE ZMB Q3464. (a) parapodium 33; (b) parapodium 130; (c) heterogomph falciger, parapodium 33, neuropodium, subacicular fascicle.

***Perinereis nigropunctata*** (Horst)

Fig.10a-e

*Nereis nigro-punctata* Horst, 1889: 171, pl.8 figs 1-3.
*Perinereis nigro-punctata.*–Gravier, 1901: 188-191, figs 190-193, table 2, pl. 11 fig.49.
*Perinereis marjorii* Southern, 1921: 595-597, figs 7, 8a-c, pl.23 fig.10 A-G.
*Nereis* (*Perinereis*) *yorkensis* Augener, 1922a: 24, fig.6a-e (fide Hartman, 1959).
*Nereis* (*Perinereis*) *nigropunctata.*–Horst, 1924: 171.
*Perinereis nigropunctata.*–Monro, 1931a: 16.–Fauvel, 1932: 107.–Fauvel, 1953: 210, fig.107b-f.–Day 1957: 84.–Day, 1962: 640.–Day, 1967: 337, fig.14.13r-v.–De Silva, 1965: 214.–Wu, 1967: 64-66, fig.9a-d.–Reish, 1968: 218.–Gibbs, 1971: 150.–Ben-Eliahu, 1972: 222.–Rullier, 1972: 90.–Hartmann-Schröder, 1979: 116-117, figs 203-206.
*Perinereis striolata.*–Hylleberg *et al.*, 1986: 10-13, fig.6A-O. (not Grube, 1878).

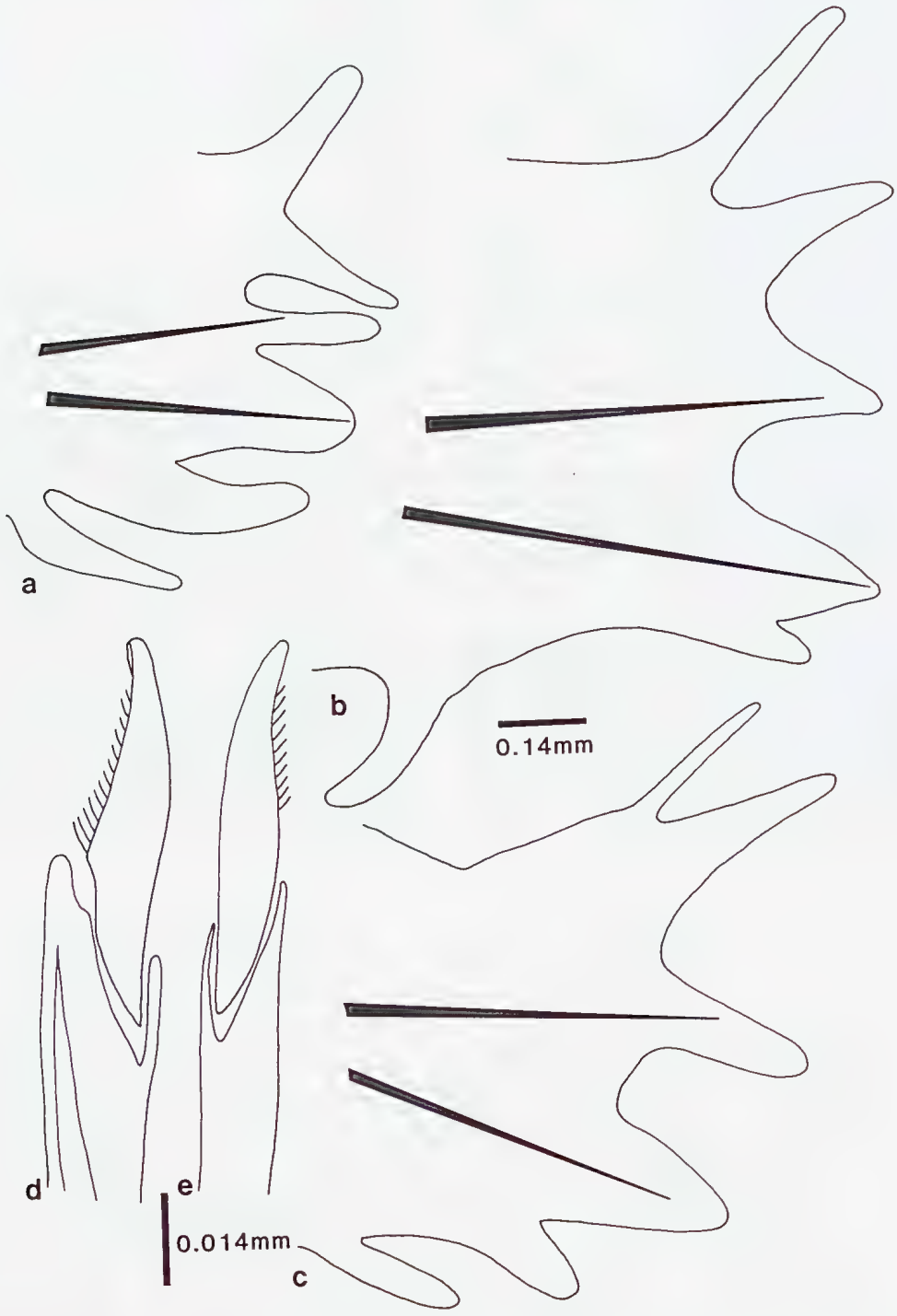


**Fig.10.** *Perinereis nigropunctata* AM W202565. (a) parapodium 3; (b) parapodium 10; (c) parapodium 50; (d) heterogomph falciger, parapodium 10, neuropodium, subacicular fascicle; (e) heterogomph falciger, parapodium 50, neuropodium, subacicular fascicle.

**Material examined.** Australia: Queensland – Cape York, SYNTYPE *Nereis* (*Perinereis*) *yorkensis*, 1 (HZM V9320); Western Australia – Dampier, 20°39'S 116°43'E, 26 June 1980, 1 (AM W202561); Gantheaume Point, 17°59'S 122°11'E, 31 July 1982, several (WAM 446-86); Broome, 17°58'S 122°13'E, 31 Oct. 1970, 1 (AM W4958); Willie Creek, 17°46'S 122°12'E, 2 Oct. 1984, 1 (NTM W2176), 20 Oct. 1984, 1 (NTM W2229); Fenelon Island, 14°08'S 125°04'E, 15 July 1988, 2 (AM W202979); East Montalivet Island, 15°06'S 125°18'E, 43 (AM W202982); Condillac Island, 14°06'S 125°33'E, 16 July 1988, 12 (AM W202981). Northern Territory – Buchanan Island, 11°49'S 130°39'E, 18 Nov. 1982, 1 (NTM W434). Queensland – Torres Strait, Prince of Wales Island, 10°41'S 142°09'E, 1 July 1976, 1 (AM W202559), July 1976, 2 (AM W202566), 2 July 1976, 1 (AM W202568); Putta Putta Beach, 10°45'S 142°36'E, 2 July 1976, 4 (AM W202565); Cape Yorke Peninsula, 11°37'S 142°38'E, 10 July 1976, 3 (AM W202560); Lizard Island, 14°40'S 145°28'E, 7 Mar. 1986, 4 (AM W202564); Trinity Inlet, 16°58'S 145°47'E, 9 Oct. 1970, 2 (AM W202567), 10 Dec. 1974, 1 (QM GH3915); Ross River, 19°22'S 146°44'E, 1 Oct. 1970, 1 (AM W4973); Mackay, 21°09'S 149°11'E, 24 Sept. 1970, 1 (AM W4928), 1 (AM W4948); Rockhampton, 23°22'S 150°32'E, Nov. 1917, 4 (AM W449); Gladstone, Calliope River, 23°55'S 151°10'E, 28 Jan. 1978, 1 (AM W202996).

**Description.** Material examined up to 180 mm length, 5 mm width, 0.7-4 mm in jaw length, 171 setigers maximum. Colour in alcohol cream-coffee brown with brown pigmentation on dorsum of some specimens. Prostomium trapezoidal with deep median furrow anteriorly, eyes small, with distinct lenses. Palps with robust, short palpophores and globular palpostyles. Antennae short, triangular. Longest tentacular cirri usually extend to setiger 3. Peristomium relatively long. Jaws robust, heavily sclerotised with approximately 7 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Areas VI, arranged as follows: I=4-9, II=12-39 in 2 curved rows; III=21-35 sometimes with 2-3 cones displaced laterally, separate from main group; IV=18-42, V=3 in triangle (very rarely 1), VI=1 bar, VII-VIII=32-46 in 2 rows. Area IV without bars. Paragnaths on oral ring tend to be larger than those on maxillary ring.

Anterior notopodia subtriangular, notopodial ligules conical, median ligules with small, superior lobes. Dorsal cirrus as long as dorsal notopodial lobes on anterior setigers, slightly longer than notopodial lobes posteriorly. Neuropodia with digitiform superior lobe; low, rounded inferior lobe; shorter postsetal lobe with straight border. Neuropodia similar in shape throughout all setigers. Ventral ligule elongate, digitiform, longer than remaining notopodial ligules, ventral cirrus approximately half as long as ventral ligule. Dorsal notopodial ligule increasing in length and greatly expanded in posterior setigers with dorsal cirrus distally inserted (Fig.10a,b).

Neurosetae with homogomph spinigers and 1-3 robust heterogomph falcigers in supra-acicular fascicle, heterogomph falcigers and spinigers in subacicular fascicle (Fig.10d,e). Anal cirri narrow, elongate.

**Remarks.** Male epitokes modified from setiger 16 onwards, females modified from setiger 19. Some specimens with brown pigmentation on dorsum of anterior setigers and prostomium (NTM W2176 and AM W202564).

Examination of type material of *Nereis* (*Perinereis*) *yorkensis* Augener, 1922a confirms the synonymy of that species with *P. nigropunctata*, as proposed by Hartman (1959).

Hylleberg *et al.* (1986) treated *P. nigropunctata* (along with *P. perspicillata* Grube, 1878, *P. obfuscata*, Grube, 1878, *P. marjorii* Southern, 1921, *P. yorkensis* Augener, 1922a and *P. dongalae* Horst, 1924) as a junior synonym of *P. striolata* Grube, 1878, however, as Hylleberg *et al.* did not examine type material we regard these synonymies as requiring verification.

**Habitat.** Occurs in estuaries, among mangroves, under rocks, sheltered reefs, and among oysters.

**Distribution.** Australia (northern Australia from 20°39'S 116°43'E, Dampier, WA to 23°22'S 150°32'E, Gladstone, Qld). Also from Singapore, Borneo (Labuan), Madagascar, Marshall Islands.

### *Perinereis obfuscata* (Grube)

Fig.11a-c

*Nereis* (*Perinereis*) *obfuscata* Grube, 1878: 86-87.–Horst, 1924: 173-174, pl.34, figs 5, 6.
*Perinereis cultrifera*.–Fauvel 1930: 528.
*Perinereis obfuscata*.–Monro 1931a: 16-18, fig.10a-d.
*Nereis obfuscata*.–Ehlers, 1920: 51.
*Perinereis striolata* Hylleberg *et al.*, 1986: 10-13, fig.6A-O.
*Perinereis cultrifera* var. *obfuscata* Monro, 1939: 398-399.

**Material examined.** Philippines: no further data, vial labelled "HOLOTYPE or SYNTYPE" (WMNA 313).

Australia: Northern Territory – Port Bremner, Danger Point, 11°07'S 132°20'E, 30 May 1982, 4 (NTM W217); Port Essington, Coral Bay, 11°11'S 132°03'E, 16 May 1983, 10+ (NTM W401). Queensland – Cape Yorke Peninsula, 11°37'S 142°38'E, 12 July 1976, 1 (AM W202817); Lizard Island, 14°40'S 145°28'E, Jan. 1977, 10 (AM W202571), June 1977, 2 (AM W202572), Jan. 1977, 20 (AM W202814), 1976, 7 (AM W203050), 17 Jan. 1976, 2 (AM W203051), 30 Dec. 1985, 1 (AM W203052); Cooktown, 15°28'S 145°15'E, 26 June 1973, 1 (AM W202816); Mackay, 21°09'S 149°11'E, 24 Sept. 1970, 1 (AM W202570). Western Australia – Dampier, 20°39'S 116°43'E, 3 Mar. 1987, 2 (AM W202815); Irvine Island, 16°05'S 123°33'E, 1 (AM W202991); Port George IV Island, 15°20'S 124°39'E, 12 July 1988, 1 (AM W202978); East Montalivet Island, 15°06'S 125°18'E, 16 July 1988, 8 (AM W202983), Bernoulii Island, 15°00'S 124°47'E, 12 July 1988, 2 (AM W202999); Descartes Island, 14°11'S 125°04'E, 20 July 1988, 1 (AM W202990); Cassini Island, 13°57'S 125°37'E, 18 July 1988, 2 (AM W203090).

**Description.** Material examined up to 15 mm length, 2 mm width, 0.5-2.0 mm in jaw length, 63 setigers

maximum. Colour in alcohol cream, often with brown pigmentation on prostomium and 3 transverse patches on anterior dorsal setigers. Prostomium trapezoidal with shallow anterior median furrow. Palps with cylindrical palpophores, rounded palpostyles. Longest tentacular cirri extending to setiger 1. Peristomium relatively long. Jaws with approximately 7 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Area VI, arranged as follows: I=2-9, II=7-27 in 2-3 crescent-shaped rows (usually between 10-20), III=13-32, sometimes with 1-2 cones displaced laterally, separate from the main group, IV=10-31, V=1 (very rarely 2), VI=1 short crescent-shaped bar, VII-VIII=22-38 in 2 rows. Area IV without bars.

Anterior notopodia with subtriangular notopodial ligules, slightly shorter, conical median ligules. Superior notopodial lobes present. Dorsal cirrus slightly longer than dorsal notopodial ligule. Dorsal notopodial ligule longer than remaining ligules. Neuropodia with digitiform superior lobe and conical inferior lobe, approximately equal in length. Postsetal lobe slightly convex, shorter than superior and inferior lobes. Ventral ligule conical, ventral cirrus two thirds to three quarters as long as ventral ligule (Fig.11a).

Notopodial ligule of median and posterior notopodia enlarged, triangular, approximately twice as long as superior and inferior neuropodial lobes. Dorsal cirrus distally inserted on posterior setigers, extending slightly beyond tip of notopodial ligule. Ventral neuropodial ligules elongate, triangular, ventral cirrus three quarters as long as ventral ligule (Fig.11b).

Neurosetae with homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph falcigers and few heterogomph spinigers in subacicular fascicle (Fig.11c).

**Remarks.** Male epitokes are modified from setiger 14 to 15 onwards, and females are modified from setiger 18 to 19. In December 1985 a number of epitokous specimens were collected using a dipnet and torchlight in Lizard Island Lagoon, Queensland (AM W203052). Non-epitokous forms were collected in January 1976 at Lizard Island among encrusting and nestling coral block fauna (AM W203050), (AM W203051).

Monro (1931a) distinguished *Perinereis obfuscata* from *P. cultrifera* by the position of epitokal modification, but subsequently (Monro, 1939) he refers to *P. obfuscata* as a variety of *P. cultrifera*. Until a detailed analysis of geographic variation is carried out, we prefer to retain *P. obfuscata* as a distinct species.

**Habitat.** Occurs on intertidal mud flats, under rocks and encrusting fauna.

**Distribution.** Australia (northern Australia from 11°07'S 132°20'E, Port Bremner, NT to 21°09'S 149°11'E, Mackay, Qld). Also from the Philippines*.

### *Perinereis pseudocamiguina* Augener

Fig.12a-c

*Nereis* (*Perinereis*) *camiguina* Augener, 1922b: 183-186, fig.5a-f, tafelfig. 3.

**Material examined.** Chile: Juan Fernandez Islands, 34°S 80°W, "zwischen röhren von Vermetiden", Jan. 1894, coll. Plate, 17 SYNTYPES, (ZMB 3726); Juan Fernandez, "ex Museum Stockholm", 5 SYNTYPES, HZM V9257.

**Description.** All syntypes entire, from 45 setigers, 11 mm length, 0.8(1.2) mm width, jaw length 7 mm to 79 setigers, 51 mm length, 2.4(3.3) mm width, jaw length 23 mm. Colour in alcohol pale brown with no obvious pigmentation patterns. Prostomium as long as wide. Antennae half as long as prostomium. Longest tentacular cirri extend to setigers 2-3. Jaws with 4-5 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Area VI, arranged as follows: I=1-2 (usually 2), II=8-16 (usually 10-14), III=7-13 (no separate lateral groups), IV=10-30 cones and 0-2 smooth bars, V=3-4 (usually 3), VI=1 straight bar, VII-VIII=39-54 in 2 rows. Bars are present on Area IV in 6 of 22 specimens.

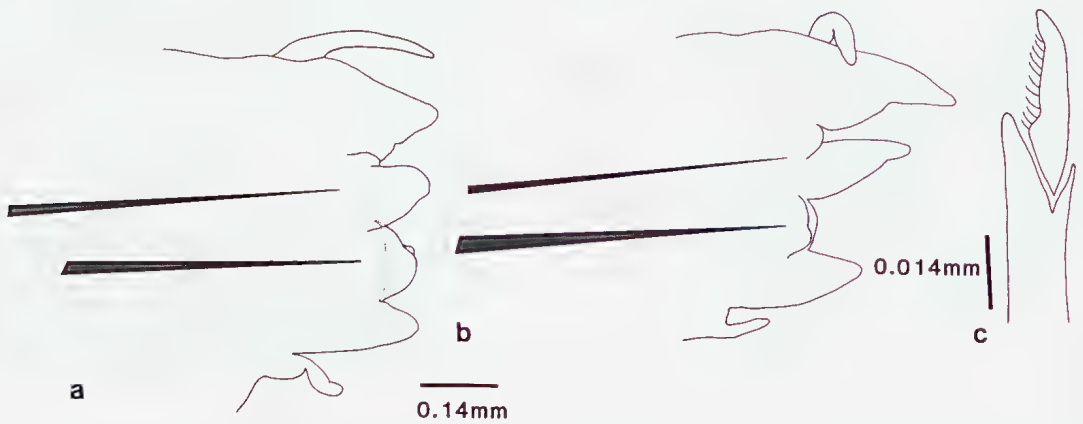


**Fig.11.** *Perinereis obfuscata* SYNTYPE WMNH 313. (a) parapodium 10; (b) parapodium 50; (c) heterogomph falciger, parapodium 50, neuropodium, subacicular fascicle.

Anterior notopodia with 2 equal subtriangular lobes. Dorsal cirrus about twice as long as dorsal notopodial lobe. Anterior neuropodia with 2 lobes, acicular ligule as long as notopodial lobes and with postsetal lobe. Ventral neuropodial ligule about three quarters as long as acicular lobe (Fig.12a). Ventral cirrus two thirds to three quarters as long as median ligule (Fig.12b). Dorsal notopodial lobe greatly expanded on posterior setigers, about 2-3 times as long as inferior notopodial lobe. Dorsal cirrus distally inserted on posterior setigers, extending beyond tip of dorsal notopodial ligule. Median and ventral neuropodial lobes similar in length. Ventral cirrus three quarters as long as ventral neuropodial ligule.

Neurosetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicle (Fig.12c), heterogomph falcigers and heterogomph spinigers (present from setiger 1) in subacicular fascicle.

**Remarks.** *Perinereis pseudocamiguinoides* is similar to another Group 1B species (see Appendix), *P. amblyodonta* (Schmarda, 1861), but can be distinguished from that species by having fewer paragnaths on Areas II, III and IV, and in lacking separate lateral groups of paragnaths on Area III.

**Distribution.** Chile (Juan Fernandez Islands*).

### *Perinereis pseudocavifrons* Fauvel

Fig.13a-f

*Perinereis pseudocavifrons* Fauvel, 1930: 529-532, fig.5.

**Material examined.** New Caledonia: "No. 41", 1928, coll. M. Pruvot, 1 SYNTYPE (MNHN UB306); Kuto, Iles des Pines, 1928, coll. M. Pruvot, 1 SYNTYPE (MNHN Bocal A98).

**Description.** Both specimens anterior fragments, 48-62 setigers, 15 mm length, 1.0(1.5) mm width, jaw length 13 mm. No pigmentation. Prostomium as long as wide. Antennae two thirds as long as prostomium. Tentacular cirri extend back to setiger 3. Jaws translucent amber, with 5-6 lateral teeth. Pharynx with conical paragnaths on both rings, smooth bars also present on Area VI, arranged as follows: I=0-2, II=4-6, III=6-9 (no separate lateral groups), IV=8-11 cones, V=0, VI=1 long bar, VII-VIII=18-24 in 2 rows. Bars absent from Area IV.

Anterior notopodia with 2 lobes similar in length, and dorsal cirri 1.25 times as long as notopodial lobes. Anterior neuropodia with 2 lobes, ventral ligule 1.25 times as long as acicular-postsetal lobes on anterior 20-25 setigers. Ventral cirri about as long as ventral ligule (Fig.13a,b,c). Dorsal notopodial lobe greatly expanded on posterior setigers, 2-3 times as long as median notopodial lobe from about setiger 50 (Fig.13d). Neuropodial lobes similar in length on posterior setigers. Both specimens incomplete posteriorly.

Neurosetae homogomph spinigers and heterogomph falcigers in the supra-acicular fascicle, heterogomph falcigers and heterogomph spinigers (present from setiger 1) in subacicular fascicle (Fig.13e,f).

**Remarks.** We have provided the above redescription because the original (Fauvel, 1930) omits some information that we consider to be of taxonomic value: presence/absence of lateral groups on Area III and of bars on Area IV on the pharynx, and the presence of heterogomph spinigers in early parapodia.

**Habitat.** Unknown.

**Distribution.** New Caledonia*.

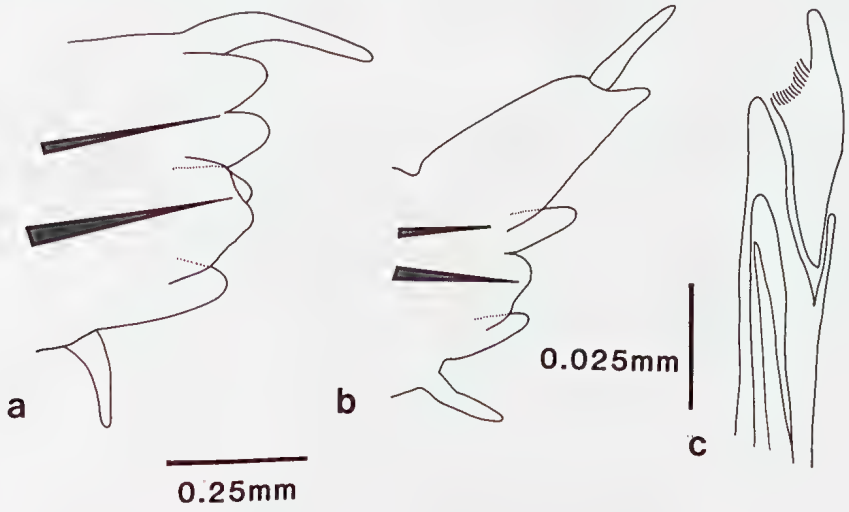


**Fig.12.** *Perinereis pseudocamiguina* SYNTYPE ZMB 3726. (a) parapodium 10; (b) parapodium 63; (c) heterogomph falciger, parapodium 10, neuropodium, supra-acicular fascicle.

***Perinereis seurati*** Gravier

Fig.14a-g

*Nereis* (*Perinereis*) *seurati* Gravier, 1905: 243-247.

**Material examined.** South Pacific Ocean: Gambier Island, Taumotu Archipelago, 23°S 135°E, coll. L.G. Seurat, 1903, 9 PARATYPES, (MNHN Bocal A98 bis).

**Description.** Size range of paratypes: 86 setigers, 48 mm length, 1.8(3.0) mm width to 122 setigers, 103 mm length, 2.5(3.6) mm width (entire specimens). Prostomium as long as wide, antennae half as long as prostomium. Eyes black. Longest tentacular cirri extend back 9-12 setigers. Jaws dark brown, with about 6 teeth.

Pharynx with conical paragnaths on both rings, smooth bars also present on Area VI, arranged as follows: I=1-2 (usually 2), II=5-10, III=9-13, including 1-2 in separate lateral groups, IV=9-15 cones, V=2-3 (usually 3), VI=1-2 bars, VII-VIII=27-31 in 2 rows. Bars absent from Area IV.

Anterior notopodia with 2 lobes of similar length, dorsal cirrus about 1.25 times as long as notopodial lobes. Neuropodia anteriorly with 2 lobes, ventral ligule about 1.25 times as long as acicular lobe (Fig.14a,b). Superior neuropodial lobe with digitiform presetal and postsetal process on anterior 20 setigers, absent posteriorly. Posterior notopodia with 2 lobes, dorsal lobe barely longer than ventral lobe, dorsal cirrus basally inserted and as long as dorsal lobe. Posterior neuropodia with 2 lobes about equal in size, and about three quarters as long as notopodial lobes (Fig.14c,d). Ventral cirri about three quarters as long as neuropodial lobes throughout. Anal cirri extend back 3-4 setigers.

Neurosetae homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph

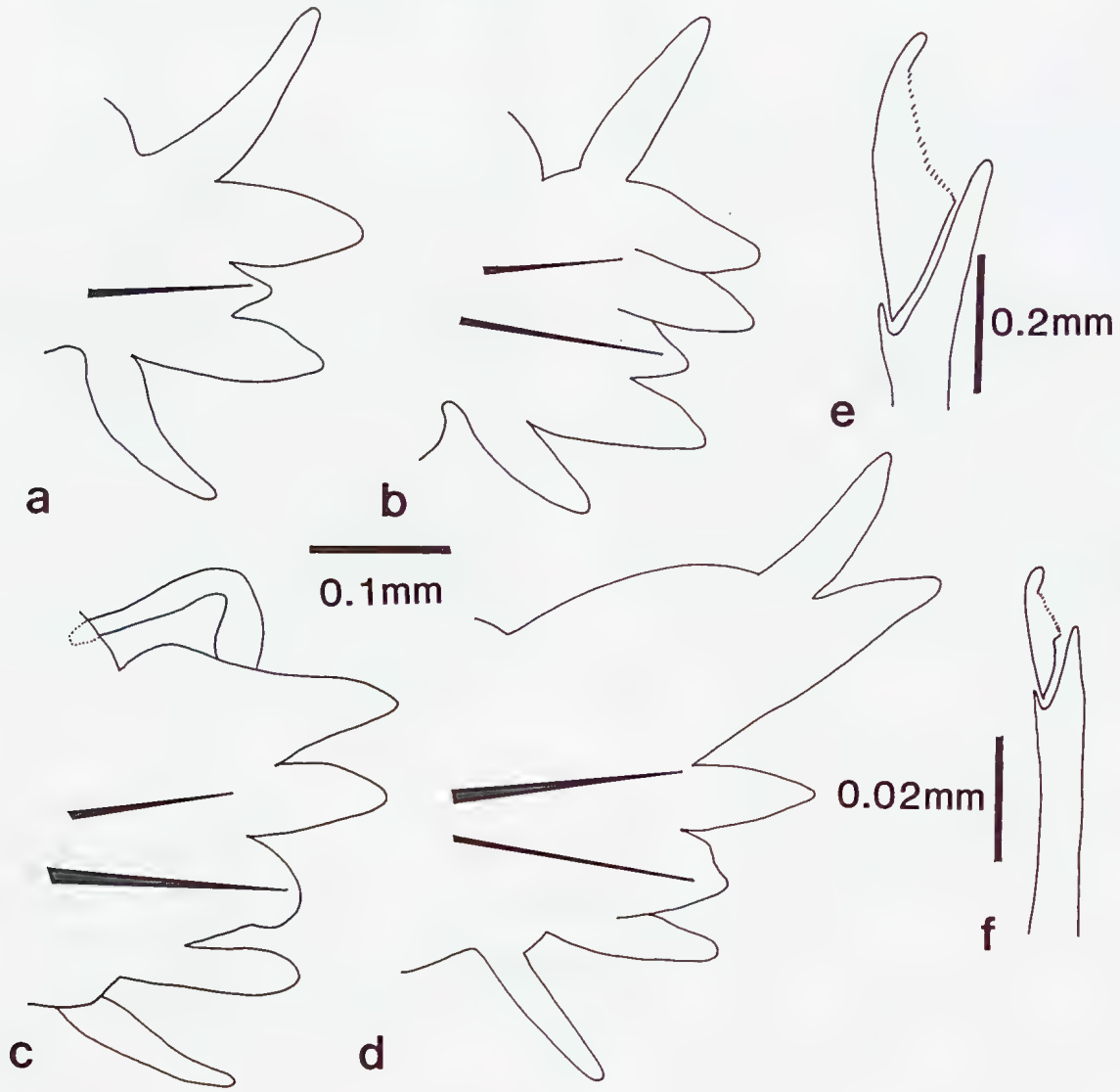


**Fig.13.** *Perinereis pseudocavifrons* SYNTYPE MNHN Bocal A98. (a) parapodium 1; (b) parapodium 3; (c) parapodium 25; (d) parapodium 47; (e) heterogomph falciger, parapodium 3, neuropodium, subacicular fascicle; (f) heterogomph falciger, parapodium 25, neuropodium, subacicular fascicle.

falcigers and heterogomph spinigers (present from setiger 1) in subacicular fascicle (Fig.14e,f).

Modified parapodia in epitoke commence from setiger 22 (Fig.14g).

**Remarks.** *Perinereis seurati* is unusual among species of *Perinereis* in that the number of bars present on Area VI of the pharynx is variable, specimens with either 1 or 2 bars being equally

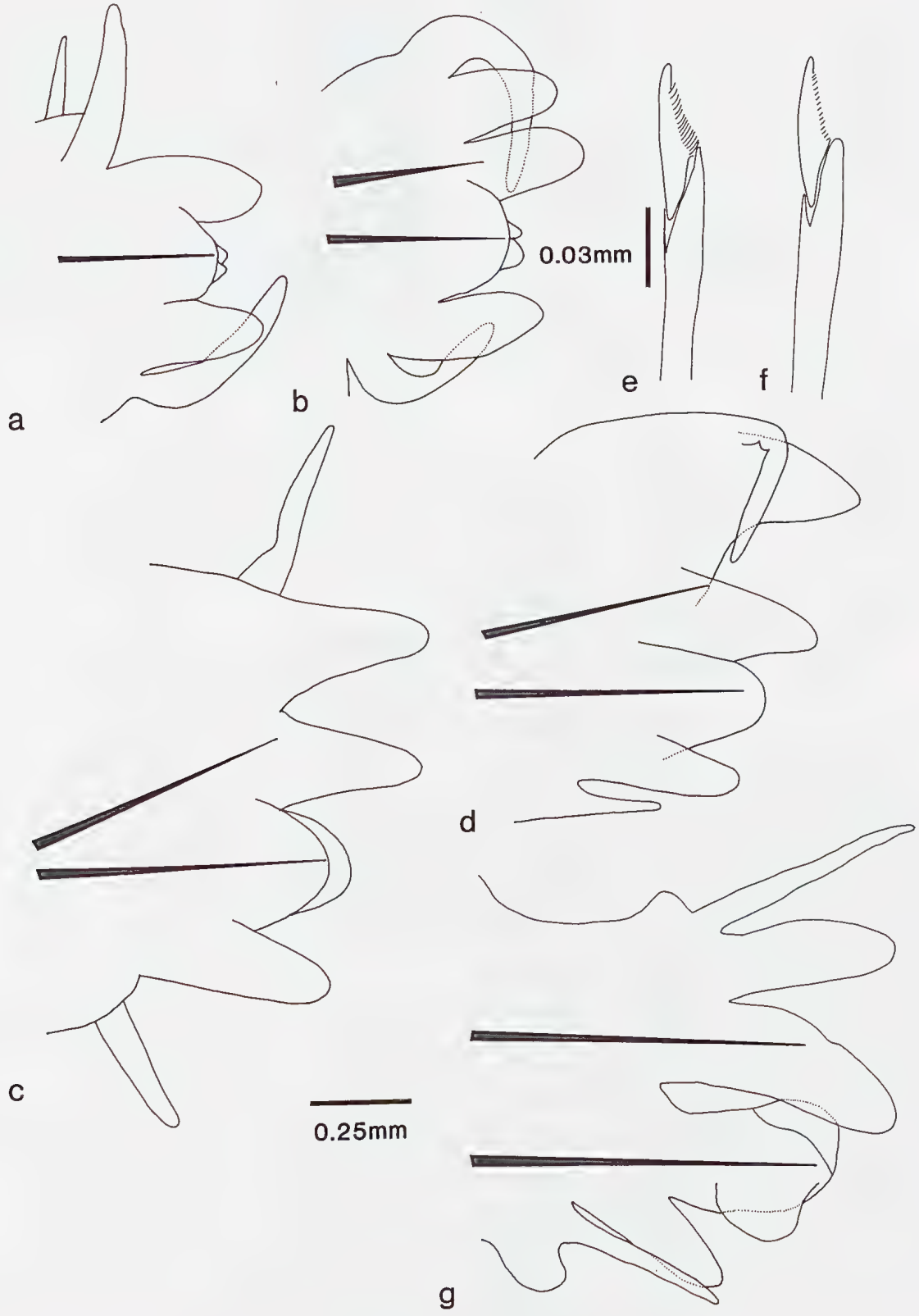


**Fig.14.** *Perinereis seurati* PARATYPE MNHN Bocal A98 bis. (a) parapodium 1; (b) parapodium 3; (c) parapodium 50; (d) parapodium 110; (e) heterogomph falciger, parapodium 110, neuropodium, subacicular fascicle; (f) heterogomph falciger, parapodium 3, neuropodium, subacicular fascicle; (g) parapodium 49, epitoke.

common.

Augener (1924b) synonymised *P. seurati* with *P. camiguina* Grube, however this species has fewer oral ring paragnaths, particularly on Area II, and also appears to be unique in having either 1 or 2 bars on Area VI. We followed earlier workers in synonymising *P. camiguina* with *P. helleri* Grube (see above), but retain *P. seurati* as a distinct species.

**Habitat.** Freshwater.

**Distribution.** Known only from Gambier Island*.

### *Perinereis singaporiensis* Grube

Fig.15a-e

*Nereis* (*Perinereis*) *singaporiensis* Grube, 1878: 84-85.–Horst, 1924: 169-170, pl.34 figs 1-2.

*Perinereis singaporiensis*.–Pruvot, 1930: 55-56, pl.3 figs 62-64.–Fauvel, 1932: 103.–Wu, 1967: 67-68.–Hylleberg, *et al.*, 1986: 9-10, fig.5A-K.

**Material examined.** Singapore no further data, 1 type (WMNH 316).

Australia: Northern Territory – Buchanan Island, 11°49'S 130°39'E, 18 Nov. 1982, 1 (NTM W429), 1 (NTM W430), 1 (NTM W435), 1 (NTM W436); Darwin, East Arm, 12°30'S 130°55'E, 21 Oct. 1983, 1 (NTM W1427), 31 Jan. 1984, 1 (NTM W1631), 1 (NTM W1646); Lee Point, 12°20'S 130°54'E, 13 Dec. 1981, 1 (NTM W73); Cape Hotham, Escape Cliffs, 12°04'S 131°18'E, 26 May 1985, 1 (NTM W2877); Adelaide River, 12°28'S 131°21'E, 20 May 1985, 1 (NTM W2901), 1 (NTM W2902), 1 (NTM W2904), 1 (NTM W2905), 23 May 1985, 1 (NTM W3013), 1 (NTM W3014), 1 (NTM W3015), 1 (NTM W3016), 12 Nov. 1985, 2 (NTM W3279); Port Essington, Victoria Settlement, 11°16'S 132°09'E, 12 Nov. 1985, 1 (NTM W3282), 2 (NTM W3284), 1 (NTM W3296),

**Fig.15.** *Perinereis singaporiensis* NTM W2600. (a) parapodium 3; (b) parapodium 10; (c) parapodium 25; (d) parapodium 50; (e) heterogomph falciger, parapodium 10, neuropodium subacicular fascicle.

2 (NTM W3298), 1 (NTM W3304), 1 (NTM W3306); Port Essington, Mangrove Point, 11°24'S 132°11'E, 15 Nov. 1985, 1 (NTM W3201), 1 (NTM W3208); Minimini Creek, 11°43'S 132°39'E, 19 June 1984, 3 (NTM W1786), 1 (NTM W1787), 2 (NTM W1790); Oxley Island, 10°59'S 132°50'E, 20 Oct. 1982, 1 (NTM W425); Annesley Point, 11°24'S 132°51'E, 19 June 1984, 1 (NTM W2062). Western Australia – Shirley Island 16°17'S 123°26'E, 26 July 1988, 1 (AM W203026); Irvine Island, 16°05'S 123°33'E, July 1988, 1 (AM W203025); Wyndham, 15°28'S 128°06'E, 26 Mar. 1985, 1 (NTM W2599), (NTM W2600); Wyndham, Parry Creek, 15°37'S 128°17'E, 24 Mar. 1985, 1 (NTM W2609), (NTM W2626); Coronation Island, 15°05'S 124°56'E, 13 July 1988, 1 (AM W203027).

**Description.** Material examined 12 mm-58 mm length, 0.5-3.5 mm width, 0.6-2.2 mm, jaw length, 144 setigers maximum. Colour in alcohol cream with a longitudinal brown pigmentation stripe on dorsum of anterior and median setigers, fading posteriorly. Prostomium trapezoidal, elongate, rectangular anteriorly. Eyes with distinct lenses. Palps with small round palpostyles. Antennae triangular. Longest tentacular cirri extending to setiger 4. Peristomium relatively long. Jaws with 6-7 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Area VI, arranged as follows: I=1-2, II=7-21, III=14-41 in a central patch with up to 8 cones laterally placed, separate from this group, IV=14-36, V=3, VI=2, VII=34-56 in 2 rows. Paragnaths on the maxillary edge of the oral ring smaller than those in the oral or posterior position. Area IV without bars.

Anterior notopodia with conical dorsal and median ligules of equal length. Superior lobes absent. Dorsal cirrus slightly shorter than dorsal ligule. Neuropodia with digitiform acicular and slightly shorter, rounded postsetal lobes. Ventral ligule dome-shaped, ventral cirrus one half to two thirds as long as ventral ligule. Median and posterior notopodia with triangular ligules longer than neuropodial lobes. Dorsal notopodial ligule glandular, dorsally convex in posterior setigers, longer than median ligules, but not greatly expanded. Dorsal cirrus shorter than dorsal ligule. Other parapodial lobes posteriorly similar to anterior setigers (Fig.15a-d). Anal cirri fine, tapering, extend back for 6 setigers.

Neurosetae with homogomph spinigers and heterogomph falcigers in the supra-acicular fascicle, heterogomph spinigers and heterogomph falcigers in the subacicular fascicle (Fig.15e).

**Remarks.** The type material examined was in poor condition and has been dehydrated at some stage. While the type specimen was in too poor condition on which to base the expanded description of this species, the type material does agree with the above description with regards to the paragnath count and distribution, setal types and number of setal lobes, although their shape is indeterminable. Material reported by Horst (1924) from Indonesia, Pruvot (1930) from New Caledonia, Fauvel (1932) from India and Wu (1967) from Taiwan apparently all refer to the same species although this material has not been examined. This is the first record of *P. singaporiensis* from Australia.

A single specimen from Western Australia (AM W203027) was found to possess two cones on Area VI of the pharynx in addition to bars. The same characteristic has been observed in some material by Horst (1924), Pruvot (1930) and Wu (1967).

**Distribution.** Australia (northern Australia from 16°17'S 123°26'E, Shirley Island, WA to 15°05'S 124°56'E, Coronation Island, NT). Also from India, Indonesia, Philippines*, Taiwan and New Caledonia.

### *Perinereis suluana* (Horst)

Fig.16a-f

*Nereis* (*Perinereis*) *suluana* Horst, 1924: 175, pl.33 fig.9.-Monro, 1926: 318.
*Perinereis suluana*.-Fauvel, 1932: 102-103.

**Material examined.** Australia: Western Australia – Dampier Archipelago, Roly Rock, 20°30'S 116°30'E, 27 Mar. 1987, 1 (AM W203030), 31 Mar. 1987, 9 (AM W203034), 3 (AM W203036), 27 Mar. 1987, 3 (AM W203037); Kendrew Island, 20°29'S 116°37'E, 28 Mar. 1987, 20 (AM W203029), 3 (AM W203032), 25 Mar. 1987, 2 (AM W203035); Brigadier Island, 20°27'S 116°37'E, 3 Apr. 1987, 3 (AM W203028); Port George IV Island, 15°20'S 124°39'E, July 1988, 3 (AM W203089); Lucas Island, 15°16'S 124°29'E, 24 July 1988, 1 (AM W203031); East Montalivet Island, 15°06'S 125°18'E, 15 July 1988, 3 (AM W203033).

**Description.** Material examined up to 35 mm length, 1.8 mm width, 1.1-1.7 mm jaw length, 70 setigers maximum. Colour in alcohol cream with olive-brown to tan pigmentation on tentacular cirri, anal cirri, edges of prostomium, dorsolateral edges of peristomium and on dorsum of setigers from setiger 2. First setiger without pigment. A darker brown pigmentation patch present in medioventral position on anterior side of first 10-15 parapodia. Dorsal pigmentation consists of 2 transverse bands; anteriormost band narrower than posterior band on each setiger. Transverse bands fade posteriorly, broader posterior band absent from median to posterior setigers, anterior band becoming narrower, persisting as 2 transverse bands in median and posterior setigers. Prostomium narrow, trapezoidal with anterior median furrow. Eyes black with distinct lenses, posterior pair round, anterior pair ovoid. Palps cylindrical, with globular palpostyles. Antennae leaf-shaped. Longest tentacular cirri extending to setiger 3 or 4. Peristomium relatively long. Jaws robust with approximately 6-7 teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Area VI arranged as follows: I=1-4 (usually 2), II=6-17, III=7-21, IV=9-22, V=0, VI=1 short rhomboidal paragnath, VII-VIII=0. Area IV without bars. Paragnaths long and slightly recurved (particularly those on Area II).

Anterior notopodia with triangular dorsal ligules, and

shorter, subconical median ligules, superior lobes absent. Dorsal cirrus as long as dorsal notopodial ligule. Neuropodia with low, rounded acicular and postsetal lobe. Ventral ligule subconical, as long as median ligule, ventral cirrus fine, tapering, three quarters as long as ventral ligule (Fig.16a-c). Median and posterior notopodia with dorsal notopodial ligule greatly expanded, triangular in posterior setigers (Fig.16d). Other parapodial lobes posteriorly similar to anterior setigers.

Neurosetae homogomph spinigers and heterogomph falcigers in the supra-acicular fascicle, heterogomph spinigers and heterogomph falcigers in subacicular fascicle. Falcigers short-bladed with coarsely denticulated blades, particularly in ventralmost position of subacicular fascicle (Fig.16e,f). Anal cirri short, blunt extend approximately 3-4 setigers. Pygidium long, cone-shaped.

**Remarks.** The Australian material agrees well with previous descriptions. Fauvel (1932) mentions the presence of a very small paragnath on the right side of Area VII of the pharynx. One of our specimens (AM W203029) had a single cone in addition to bar in Area VI. This species is readily identifiable by the absence of paragnaths in Areas VII-VIII and very distinctive dorsal pigmentation. (The only other species of *Perinereis* in which Areas VII-VIII are bare is *P. matthaii* Aziz, 1938 from India; see Appendix.) The variable form of the 'bars' in Area VI, however, indicates that the generic status of this species is questionable (see comments after generic definition). Two male specimens, one collected from Port George IV Island, Kimberley Group, Western Australia in July 1989 (AM W203089), and another from Kendrew Island, Dampier Archipelago in March 1987 (AM W203032) showed epitokal modification from setiger 15 onwards. Dorsal pigmentation varied from dark olive brown to light tan and tended to be very much lighter in small specimens.

**Habitat.** In dead coral substrate in 10 m depth water.

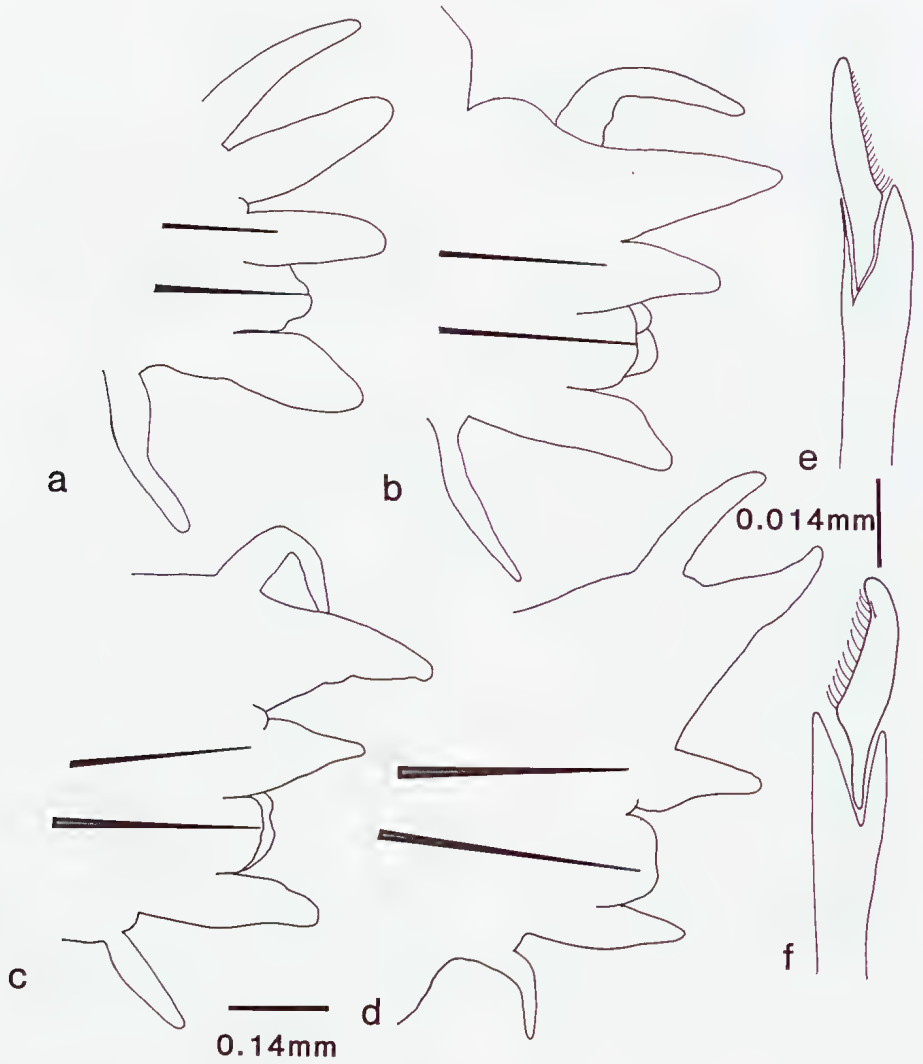


**Fig.16.** *Perinereis suluana* AM W20328. (a) parapodium 3; (b) parapodium 10; (c) parapodium 25; (d) parapodium 50; (e) heterogomph falciger, parapodium 25, neuropodium, subacicular fascicle; (f) heterogomph falciger, parapodium 50, neuropodium, subacicular fascicle.

**Distribution.** Australia (north-western WA from Roly Rock, 20°30'S 116°30'E to East Montalivet Island, 15°06'S 125°18'E). Also from Malay Archipelago, Philippines (Sulu Archipelago), Papua New Guinea (Admiralty Islands) and New Caledonia.

### *Perinereis vancaurica* (Ehlers)

Fig.17a-h

*Nereis vancaurica* Ehlers, 1868: 503, pl.20.–Ehlers, 1904: 25-26.–Fauvel, 1923: 34.

*Nereis languida*.–Grube, 1868: 15, pl.2 fig.1a-b.

*Nereis* (*Perinereis*) *vancaurica*.–Grube, 1878: 83-84.–Augener, 1922: 23-24.

*Perinereis horsti* Gravier, 1901: 182, figs 182-184, pl.11 fig.47.

*Perinereis vancaurica* Monro, 1931a:14.–Monro, 1931b: 38-41, fig.2a-f.

*Perinereis vancaurica*.–Kott, 1951: 88, 111.–Fauvel, 1932: 103.–Fauvel, 1953: 205-206, fig.105f-g.–Russell, 1962: 7.–Day 1967: 334, fig.14.12k-o.–Wu, 1967: 70-71.–Wu *et al.*, 1985: 195-197, fig.111A-J.–Rullier, 1972: 90-92.–Hartmann-Schröder, 1979: 117, figs 207-210.–Lana, 1984:

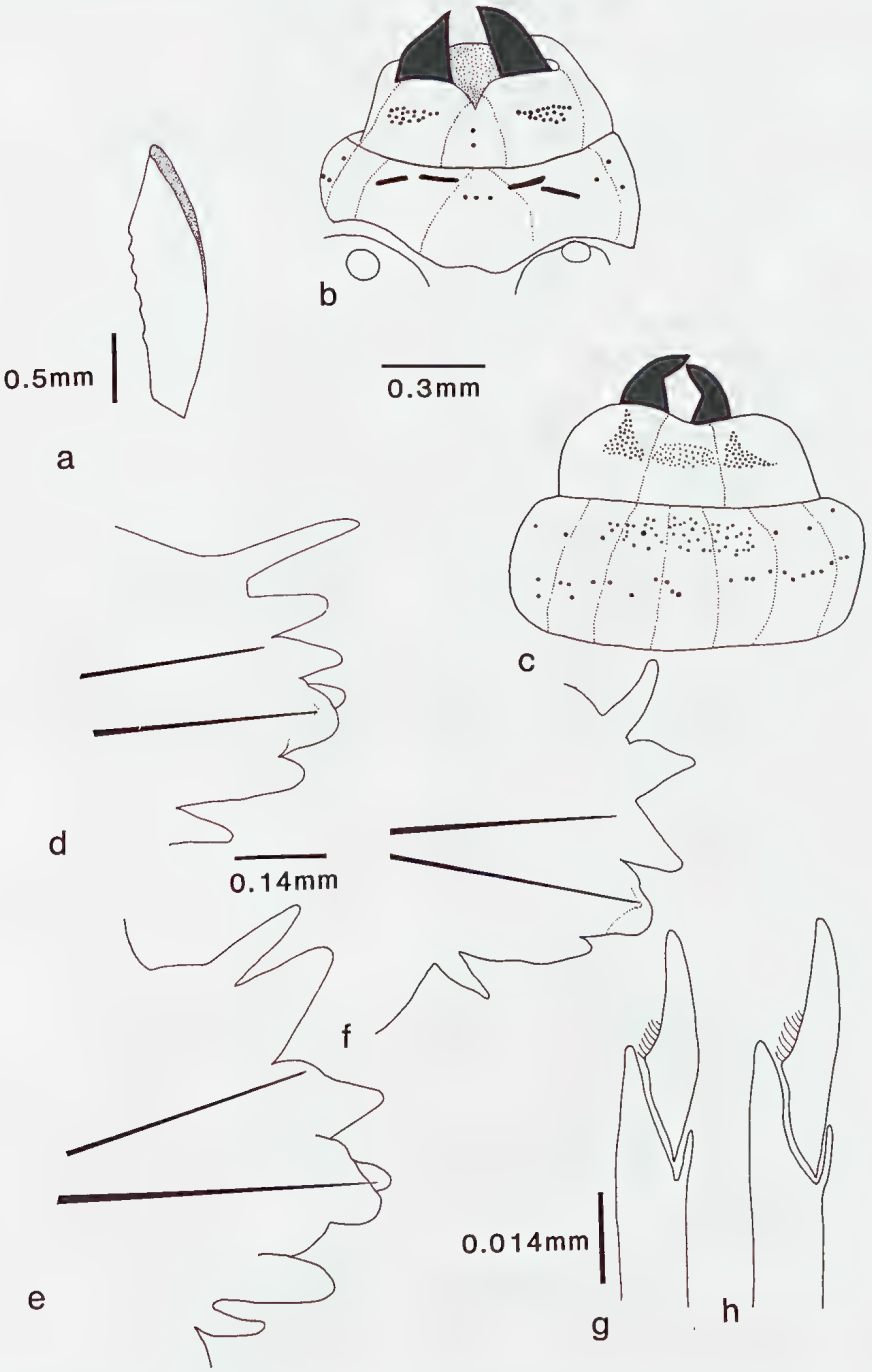


**Fig.17.** *Perinereis vancaurica* AM W202550. (a) jaw, right side WMNH 418; (b) everted pharynx, dorsal view; (c) everted pharynx, ventral view; (d) parapodium 3; (e) parapodium 10; (f) parapodium 50; (g) heterogomph falciger, parapodium 10; neuropodium, subacicular fascicle; (h) heterogomph falciger, parapodium 50, neuropodium, subacicular fascicle.

121-123.
*Perinereis vancaurica indica* Bhatt & Bal, 1966: 25.
*Perinereis linea.*–Wu, 1967: 68-69, fig.10a-d, non Treadwell, 1936.
*Perinereis vancaurica tetradentata* Imajima, 1972: 86-88, fig.23a-i.
*Perinereis* sp. Shin, 1982: 164-165, table 1.

**Material examined.** Philippine Islands, no further data, (WMNH 418, material of Grube, 1878).

Australia: Western Australia – Entrance Island, 15°17'S 124°38'E, 12 July 1988, 2 (AM W20299); Jackson Island, 15°10'S 124°28'E, 11 July 1988, 1 (AM W202980); Cornielle Island, 14°12'S 125°44'E, July 1988, 3 (AM W202825). Northern Territory – Port Keats, 14°06'S 129°33'E, 23 June 1952, 2 (AM W202550); Escape Cliff, 12°08'S 131°15'E, 26 Mar. 1985, 1 (NTM W2876), 26 May 1985, 2 (NTM W2878), 1 (NTM W2879), 1 (NTM W2880); Port Essington, Victoria Settlement, 11°16'S 132°09'E, 12 Sept. 1985 (NTM W3291), (NTM W3293); Port Bremner, Danger Point, 11°07'S 132°20'E, 30 Apr. 1982, 4 (NTM W218); Oxley Island, 10°59'S 132°50'E, 20 Oct. 1982, 1 (NTM W424); Annesley Point, 11°24'S 132°51'E, 19 June 1984 (NTM W1770), (NTM W1776), June 1984 (NTM W1772), 16 June 1984 (NTM W1806), (NTM W1811), 16 June 1984 (NTM W1827); Entrance Island 15°17'S 124°38'E, 12 July 1988, 2 (AM W202995); Vanderlin Island, 15°42'S 136°59'E, July 1923, 2 (AM W4833), (NTM W4834). Queensland – Torres Strait, Prince of Wales Island, 10°41'S 142°09'E, 29 May 1969, 1 (NMV 56468) Cairns, Yorkeys Knob, 16°49'S 145°43'E, 1 (AM W2355), 19 Nov. 1984, 2 (NTM W2361); Hervey Bay, Eli Creek, 25°17'S 152°49'E, 1 (AM W5383); Frazer Island, 25°22'S 153°07'E, 30 July 1975, 1 (QM GH3922). South Australia – Murray River Mouth, 35°34'S 138°53'E, 2 (AM W202549), 31 Dec. 1971, 1 (AM W203023).

**Description.** Material examined up to 45 mm length, 3.5 mm width, 0.9-2.1 mm in jaw length, 198 setigers maximum. Colour in alcohol, cream with light brown longitudinal, median stripe along dorsum, less distinct posteriorly. Prostomium broad, two thirds as wide as long, with shallow median furrow. Palps large, cylindrical, with small globular palpostyles. Antennae broad based. Longest tentacular cirri extending to setiger 3. Peristomium relatively short. Jaws robust, heavily sclerotised particularly on the outer lateral margin which forms flattened ridge (Fig.17a). Distalmost third of jaw with smooth edge. Cutting edge serrate rather than denticulate proximally. Pharynx with conical paragnaths on both rings and smooth bars on Area VI. Paragnaths arranged as follows: I=1-3, II=16-42, III=32-84, IV=40-88 in triangle, V=3, VI=2 long flattened bars, VII-VIII=58-129 in 2-5 rows. Paragnaths in VII-VIII in 2 bands, band closest to oral end of pharynx consists of large cones in 2 irregular rows. A separate band, (maxillary edge), contains a number of very small paragnaths interspersed with larger paragnaths in midventral position (Fig.17b,c).

Anterior notopodia with conical notopodial ligules, median ligule slightly longer than dorsal ligule, with small superior lobe. Dorsal cirrus slightly longer than dorsal ligule. Neuropodia with superior lobe poorly developed, dome-shaped inferior lobe and smaller digitiform postsetal lobe. Ventral ligule conical, shorter than inferior lobe, ventral cirrus approximately two thirds as long as ventral neuropodial ligule (Fig.17d,e).

Median and posterior notopodia with dorsal ligule triangular, broad-based. In far posterior setigers dorsal notopodial lobe slightly longer than median ligule, broad and glandular. Dorsal cirri becoming distally inserted on notopodial ligule on posterior setigers (Fig.17f). Other parapodial lobes posteriorly similar to anterior setigers.

Neurosetae with homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph falcigers and 1-2 heterogomph spinigers in subacicular fascicle (Fig.17g,h).

**Remarks.** One female epitoke collected 12 September 1985 from Victoria Settlement, Port Essington, Northern Territory (NTM W3293) was heavily pigmented with patches of dark brown pigmentation on either side of the dorsum in anterior setigers.

*Perinereis vancuarica* may be confused with *P. aibuhitensis* Grube, 1878, but the former species is distinguished by having longer bars in Area VI and in having a greater number of paragnaths in Areas II, III, IV and VII-VIII of the pharynx than in *P. aibuhitensis*.

**Habitat.** Occurs intertidally in mangroves and under oyster and barnacle encrusted rocks.

**Distribution.** Australia (northern Australia from Jackson Island, WA, 15°10'S 124°28'E to Frazer Island, Qld, 25°22'S 153°07'E); two specimens (AM W202549) and (AM W203023) from Murray River Mouth, SA (35°34'S 138°53'E). Also from the Philippines*; widely distributed in the tropical Indian and Western Pacific Oceans.

### *Perinereis variodentata* (Augener)

Fig.18a-c

*Nereis* (*Perinereis*) *variodentata* Augener, 1913: 179-182, fig.19a-c, pl.3 fig.50u.
*Perinereis variodentata.*–Kott, 1951: 112-113, fig.6a-g.–Hartman, 1954: 35.–Hartmann-Schröder, 1982: 79-80.–Hartmann-Schröder, 1983: 139.–Hartmann-Schröder, 1984: 29.–Hutchings & Turvey, 1982: 140-141.–Hartmann-Schröder, 1987: 49.

**Material examined.** Australia: Western Australia – Albany, Princess Royal Harbour, 35°00'S 117°52'E, SYNTYPE (HZM V-7923), Albany, Princess Royal Harbour, 21-22 Aug. 1905, SYNTYPE (ZMB 5276). New South Wales – Port Molle, 20°20'S 148°51'E, 1 (AM W4830); La Perouse, 33°59'S 151°15'E, 24 Oct. 1962, 1 (AM W4791); Twofold Bay, 37°05'S 149°54'E, 9 Oct. 1984, 1 (AM W202556); Twofold Bay, Munganno Point, 37°06'S 149°56'E, 19 Dec. 1985, 2 (AM W202551), 26 Mar. 1985, 1 (AM W202552), 20 Mar.

1985, 1 (AM W202553); Green Cape, 37°16'S 150°03'E, 13 Feb. 1973, 1 (AM W202557). Tasmania – Bicheno, Tinderbox, 41°53'S 147°18'E, 29 May 1974, 1 (TASM K1106); Spring Bay, 42°32'S 147°55'E, 11 Jan. 1939, 1 (AM W3587); Hobart, 42°53'S 147°19'E, 20 Feb. 1909, 1 (TASM K1000). South Australia – West Island, 35°37'S 138°36'E, 18 Jan. 1977, 1 (SAM E2381); Bay of Shoals, 35°37'S 137°36'E, Mar. 1978, 1 (AM W18341); Kangaroo Island, Snellings Beach, 35°40'S 137°05'E, 5 Mar. 1979, many (AM W18335); Hanson Bay, 36°02'S 136°51'E, 4 Mar. 1979, many (AM W18339); Thistle Island, 35°00'S 136°09'E, 11 Jan. 1977, 1 (SAM E2382); Elliston, 33°39'S 134°53'E, 11 Mar. 1979, several (AM W18334); Greenly Island, 34°39'S 134°46'E, 28 Nov. 1976, 1 (SAM E2383); Waldegrave Island, 33°36'S 134°37'E, 25 Oct. 1975, 1 (AM W18489); Baird Bay, 33°07'S 134°20'E, 27 Feb. 1975, 1 (SAM E2384). Western Australia – Frenchmans Bay, 35°05'S 117°57'E, 3 Sept. 1959, 2 (AM W 4831); Yallingup, 33°42'S 115°06'E, 2 Jan. 1972, 1 (AM W18471); Garden Island, 32°12'S 115°40'E, 1950, several (WAM 475-86); Rottnest Island, 32°00'S 115°30'E, 1946 (AM W18575); Cape Peron, 25°30'S 113°31'E, 1946, many (AM W6828); Vancouver Point, 14°50'S 128°12'E, 13 Dec. 1983, 20 (AM W202555).

**Description.** Material examined up to 47 mm length, 3.5 mm width, 0.6-2.5 mm in jaw length, long maximum number of setigers 81. Colour in alcohol cream with brown, granular, glandular structures visible on dorsum of posterior notopodial dorsal ligules and lateral edges of posterior setigers. Prostomium trapezoidal, slightly indented anteriorly. Eyes large, with distinct lenses. Palps widely spaced, dome-shaped with globular palpostyles. Antennae slightly annulated. Longest tentacular cirri extending to about setiger 9. Peristomium relatively short. Jaws robust, heavily sclerotised, with about 6 proximal teeth, distal third smooth, without teeth. Pharynx with conical paragnaths on both rings and smooth bars also present on Areas VI and occasionally IV arranged as follows: I=4-15, usually in 2 groups, those on maxillary end set in a close cluster, those on oral edge spread out, II=3-12 in 2 rows, approximately in triangle, III=1-6, IV=4-22 (sometimes with 1-2 bars), V=2-3 in a longitudinal row, VI=2 long bars and 2-4 cones, VII-VIII=40-86 in 2 rows laterally, 4-6 rows ventrally.

Dorsal and median notopodial ligules dome-shaped on anterior setigers, becoming subtriangular after the first few setigers and about equal in length. Digitiform superior notopodial lobes present. Dorsal cirrus approximately twice as long as dorsal notopodial ligule. Neuropodia with small, knob-like superior lobe, larger, rounded inferior lobe with slightly shorter low, rounded postsetal lobe. Ventral ligule conical. Ventral cirrus longer than neuropodial ligules (Fig.18a).

Median and posterior notopodial ligules conical to subtriangular with dorsal ligule gradually exceeding median ligule in length to become broader posteriorly, dorsally crescent-shaped with dorsal cirrus more distally inserted. Dorsal cirrus twice as long as notopodial ligule posteriorly.

Neuropodia as for anterior setigers with distinction between superior and inferior lobes not as pronounced posteriorly. Lobes less robust (Fig.18b).

Neurosetae with homogomph spinigers and heterogomph falcigers in supra-acicular fascicle, heterogomph spinigers and falcigers in subacicular fascicle (Fig.18c). Anal cirri long, fine.

**Remarks.** The cones which are placed on the inner edge of Area VI of the pharynx have usually been reported by other workers as being part of Area V. Specimens from Vancouver Peninsula near Mistaken Island, Albany, Western Australia (AM W202555) are deep rust coloured. Specimen (AM W3587) a female epitoke, modified from setiger 17 onwards, was collected from Spring Bay, Tasmania in January 1939.

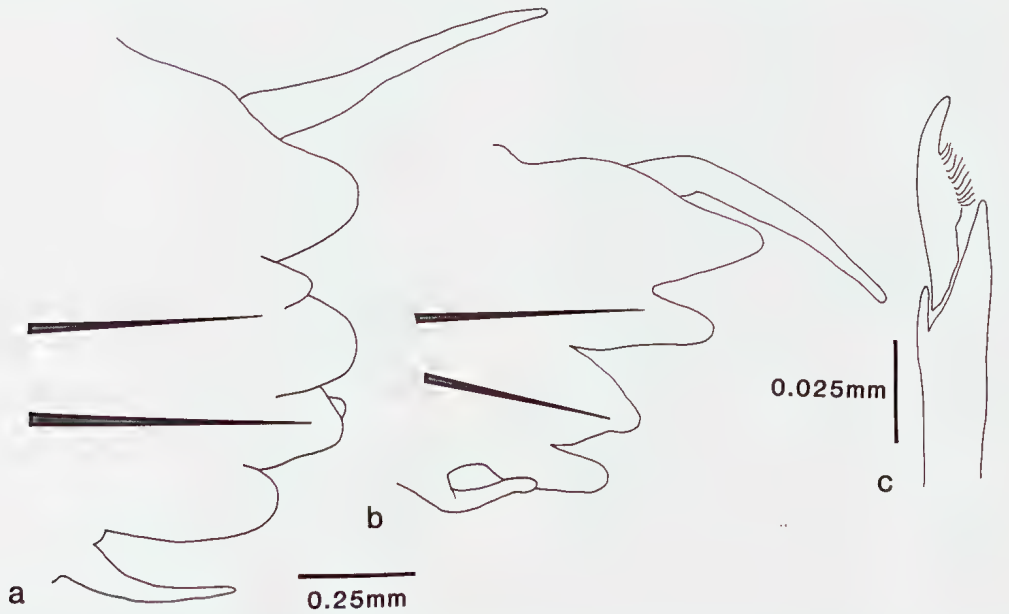


**Fig.18.** *Perinereis variodentata* SYNTYPE ZMB 5276. (a) parapodium 12; (b) parapodium 60; (c) heterogomph falciger, parapodium 12, neuropodium, subacicular fascicle.

**Habitat.** Occurs in association with encrusting fauna, among kelp holdfasts, coralline algae and in rock platform crevices.

**Distribution.** Australia (southern Australia from 20°20'S 148°51'E, Port Molle, NSW to 25°30'S 113°31'E, Vancouver Point, WA).

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## APPENDIX

Annotated list of *Perinereis* species.

This list includes an informal grouping of species of *Perinereis* according to a system similar to that proposed for *Neanthes* by Fauchald (1972). The system is as follows:

1 Area VI with 1 bar
  A Dorsal notopodial lobe not greatly expanded
  B Dorsal notopodial lobe greatly expanded on posterior setigers
2 Area VI with 2 bars
  A Dorsal notopodial lobe not greatly expanded
  B Dorsal notopodial lobe greatly expanded on posterior setigers (no species yet recorded)
3 Area VI with 3 or more bars (usually 6 or more in an arc)
  A Dorsal notopodial lobe not greatly expanded
  B Dorsal notopodial lobe greatly expanded on posterior setigers

Descriptive data in this list is based on the original description unless otherwise stated. Also included is original combination, reference to original description and type locality.

### GROUP 1A

*arabica* (*Perinereis arabica* Mohammad, 1971: 291. Persian Gulf).

*calmani* (*Nereis* (*Perinereis*) *calmani* Monro, 1926: 318-320, figs 6-8. Eastern Australia and China Sea).

*cultrifera* (*Nereis cultrifera* Grube, 1840: 74, fig.6. Naples, Mediterranean Sea).
Remarks. Redescribed above.

*dongalae* (*Nereis* (*Perinereis*) *dongalae* Horst, 1924: 174-175, pl.33 fig.8. Celebes).
Remarks. We have re-examined the holotype (ZMA VPOL 1064), which has the pharynx removed. The original description of Horst (1924) indicates that *P. dongalae* can be distinguished from *P. helleri* on the basis of having more paragnaths on Areas I and III. Hylleberg *et al.* (1986) treated *P. dongalae* as a junior synonym of *P. striolata*, however since those authors did not examine type material (which is in any case indeterminate) we prefer to retain *P. dongalae* as distinct.

*falsovariegata* (*Perinereis falsovariegata* Monro, 1933: 492, figs 4-7. Still Bay, South Africa).

*floridana* (*Nereis* (*Perinereis*) *floridana* Ehlers, 1868: 503-506. Florida, North America).

*helleri* (*Nereis* (*Perinereis*) *helleri* Grube, 1878: 81. Philippines).
Remarks. *Perinereis camiguina* Grube, 1878 is a junior synonym. See above.

*rullieri* (*Perinereis rullieri* Pilata, 1974: 25-37, figs 1-4. Sicily, Catania, Mediterranean Sea).

*taorica* (*Perinereis taorica* Langerhans, 1881: 110-111, fig. 15a-c. Canary Islands).
Remarks. The description of Langerhans (1881) suggests that *P. taorica* is close to *P. cultrifera* and related species.

*tenuisetis* (*Perinereis* (*Arete*) *tenuisetis* Fauvel, 1915: 6-9, fig.5a-f. Mediterranean Sea).

*villalobosi* (*Perinereis villalobosi* Rioja, 1947: 532-534, figs 18-22. Western Mexico).

**GROUP 1B**

*amblyodonta* (*Nereilepas amblyodonta* Schmarda, 1861: 106. New South Wales, Australia).

*anderssoni* (*Perinereis anderssoni* Kinberg, 1866: 175. Brazil).
Remarks. Hartman (1948) redescribed the type specimen. Junior synonyms include: *Nereis bairdii* Webster, 1884 (fide Hartman, 1948; Hartman, 1951); *Nereis minor* Hansen, 1882 (fide Hartman, 1948; Augener, 1934); *Nereis* (*Perinereis*) *melanocephala* McIntosh, 1885 (fide Linero Arana & Vasquez, 1979; Rioja, 1960). *Perinereis ponteni* Kinberg, 1866 was considered a synonym by Hartman (1948) but retained as a distinct species by Lana (1984).

*barbara* (*Nereis* (*Perinereis*) *barbara* Monro, 1926: 316-317, figs 3-5. New South Wales, Australia).

*elenacosoi* (*Perinereis elenacosoi* Rioja, 1947: 531-532, figs 8-17. Western Mexico).

*falklandica* (*Nereis* (*Perinereis*) *falklandica* Ramsay, 1914: 44-46, pl.3 figs 3-10. Falkland Islands).

*longidonta* (*Perinereis longidonta* Rozbaczylo & Castilla, 1973: 221-225, figs 1b, 3a-f. Chile).

*macropus* (*Nereis* (*Lipephile*) *macropus* Claparède, 1870: 444-448, pl. 8 fig.1, Naples, Mediterranean Sea).
Remarks. This species is placed in Group 1B based on the description of Ben-Eliahu, 1975: 182.

*malayana* (*Nereis malayana* Horst, 1889: 167-171, pl. 8 figs 4-7. Malay Archipelago).
Remarks. The placement of *P. malayana* in Group 1B, with dorsal notopodial lobes expanded posteriorly, is provisional since it is based on Horst (1889) who examined epitokes only. Horst's description of posteriormost setigers with parapodia similar to atokous worms seems, however, to fit Group 1B.

*marionii* (*Nereis marionii* Audouin & Milne-Edwards, 1833 [not seen]. France).
Remarks. The placement of *P. marionii* in Group 1B is based on the description of Nunez *et al.* (1981).

*monterea* (*Nereis* (*Neanthes*) *monterea* Chamberlin, 1918: 174-175. California).
Remarks. *Nereis spinifera* Treadwell, 1929 (from Puget Sound, Washington) is a junior synonym (Hartman, 1956: 281).

*nigropunctata* (*Nereis nigropunctata* Horst, 1889: 171-174, pl.8 figs 1-3. Malay Archipelago).
Remarks. See above.

*obfuscata* (*Nereis (Perinereis) obfuscata* Grube, 1878: 86-87. Philippine Islands).
Remarks. See above.

*ponteni* (*Perinereis ponteni* Kinberg, 1866: 175. Rio de Janeiro, Brazil).
Remarks. See Remarks for *P. anderssoni.*

*pseudocavifrons* (*Perinereis pseudocavifrons* Fauvel, 1930: 529-532, fig.5. New Caledonia).
Remarks. Redescribed above.

*suluana* (*Nereis* (*Perinereis*) *suluana* Horst, 1924: 175, pl.33 fig.9. Sulu Archipelago, Philippine Islands).
Remarks. See above.

*tobeloana* (*Nereis* (*Perinereis*) *tobeloana* Augener, 1933: 116-118, fig.10. Malay Archipelago).

**GROUP 1 – CONDITION OF DORSAL NOTOPODIAL LOBE NOT KNOWN**

*cavifrons* (*Nereis* (*Perinereis*) *cavifrons* Ehlers, 1920: 47-49, pl.1 figs 6-10. Java, Indonesia).
Remarks. Redescribed above.

*curvata* (*Perinereis curvata* Holly, 1935: 25-27, fig.12a-l, pl.1I. Hawaiian Islands).
Remarks. Hartman (1966) points out that this species is very close to *P. helleri.* Holly (1935) described only epitokes.

*perspicillata* (*Nereis* (*Perinereis*) *perspicillata* Grube, 1878: 90-91, pl.4 fig.10. Philippine Islands).

*striolata* (*Nereis* (*Perinereis*) *striolata* Grube, 1878: 85-86, pl.4 fig.9. Philippine Islands).

**GROUP 2A**

*aibuhitensis* (*Perinereis aibuhitensis* Grube, 1878: 89, pl.5 fig.3. Philippines).
Remarks. Dorsal notopodial lobe reduced on posterior setigers. See above.

*brevicirrata* (*Nereis brevicirrata* Treadwell, 1920: 467-468, figs 1-4. Brazil).
Remarks. Hartman (1938) recognised *P. brevicirrata* as a species of *Perinereis.*

*camiguinoides* (*Nereis* (*Perinereis*) *camiguinoides* Augener, 1922b: 180-183, fig.4a-d, tafelfig. 2. Juan Fernandez Islands).
Remarks. Redescribed above.

*kuwaitensis* (*Perinereis kuwaitensis*) Mohammad, 1970: 185. Arabian Gulf).

*jascooki* (*Perinereis jascooki* Gibbs, 1972: 207-208, fig.4a-i. Cook Islands, South Pacific).

*singaporiensis* (*Nereis* (*Perinereis*) *singaporiensis* Grube, 1878: 84-85. Singapore).
Remarks. Condition of dorsal notopodial lobe not determinable from the type, on Australian material expanded, glandular, dorsally convex in posterior setigers.

*vancaurica* (*Nereis vancaurica* Ehlers, 1868: 503, pl.20. Nicobar Islands).
Remarks. See above.

*variodentata* (*Nereis* (*Perinereis*) *variodentata* Augener, 1913: 179-182, fig.19a-c, pl.3 fig.50. South-western Western Australia).
Remarks. See above.

**GROUP 2B**

As yet no species with this condition have been described.

**GROUP 2 – CONDITION OF DORSAL NOTOPODIAL LOBE NOT KNOWN**

*aculeata* (*Nereis aculeata* Hansen, 1882: 12, pl.4 figs 13-17. Brazil).

**GROUP 3A**

*binongkae* (*Nereis* (*Perinereis*) *binongkae* Horst, 1924: 175-176, pl. 34 figs 7-8).
Remarks. See Wilson & Glasby (in preparation).

*caeruleis* (*Heteronereis caeruleis* Hoagland, 1920: 608, pl.47 figs 13-16, pl.48 figs 1-4. Philippines).
Remarks. *Perinereis neocaledonica* Pruvot, 1930 is a junior synonym; see Wilson & Glasby (in preparation).

*gualpensis* (*Perinereis gualpensis* Jeldes, 1963: 3-10, figs 1-5. Chile; freshwater).
Remarks. Bertran (1980) provided additional descriptive data and a comparison with *P. vallata.*

*majungaensis* (*Perinereis nuntia* var. *majungaensis* Fauvel, 1921: 11. Madagascar).
Remarks. See Wilson & Glasby (in preparation).

*matthaii* (*Perinereis matthaii* Aziz, 1938: 29, pl.3 fig.1, pl.6 figs 29-30, pl.7 figs 56-57. Karachi, India).
Remarks. The absence of paragnaths on Area VII-VIII is distinctive.

*mictodonta* (*Nereis mictodonta* Marenzeller, 1879: 118-119, pl.2 fig.2.
Remarks. Close to *P. nuntia* but status uncertain; see Wilson & Glasby (in preparation).

*nuntia* (*Lycoris nuntia* Savigny, 1818: 312-313. Gulf of Suez).
Remarks. *Nereis* (*Lycoris*) *quatrefagesi* Grube, 1878, *Nereis* (*Perinereis*) *heterodonta* var. *mictodontoides* Augener, 1913, *Perinereis broomensis* Hartmann-Schröder, 1979, and *P. weijhouensis* Wu, Sun & Yang, 1981 are junior synonyms; see Wilson & Glasby (in preparation).

*ponuiensis* (*Nereis* (*Perinereis*) *ponuiensis* Augener, 1924: 349-352, figs 5-6. New Zealand).
Remarks. See Wilson & Glasby (in preparation).

*rhombodonta* (*Perinereis rhombodonta* Wu, Sun & Yang, 1981[1985]: 199-201, fig.113a-j. Guandong and GuangXi, China).
Remarks. See Wilson & Glasby (in preparation).

*rumphii* (*Nereis* (*Perinereis*) *rumphii* Horst, 1919: 60-62, fig.2. Aru Islands and East Flores, Indonesia).
Remarks. See Wilson & Glasby (in preparation).

*vallata* (*Nereis vallata* Grube, 1858: 159-160. Chile, Valparaiso).
Remarks. See Wilson & Glasby (in preparation).

**GROUP 3B**

*maindroni* (*Perinereis maindroni* Fauvel, 1943: 201-202, fig.1e-i. France).

**GROUP NOT KNOWN**

*aberrans* (*Perinereis aberrans* Kinberg, 1866: 176. Type locality not known). *Nomen dubium.*
Remarks. The type material is in poor condition (Hartman, 1948); parapodia "resemble *P. cultrifera*" (i.e. dorsal notopodial lobe not expanded posteriorly?) and the arrangement of paragnaths cannot be determined. We consider this to be a *nomen dubium.*

*exsul* (*Perinereis exsul* Kinberg, 1866: 175. Type locality unknown). *Nomen dubium.*
Remarks. Hartman (1948) examined the type specimen, which was indeterminable.

## NOTE ADDED IN PRESS

Wilson & Glasby (ms submitted to Records of the Australian Museum) describe two new species of *Perinereis* which belong in Group 3A, according to the above scheme.

A forthcoming revision of the subfamily Nereidinae by one of us (Wilson, in preparation) will propose new generic combinations for many species currently placed in the genus *Perinereis*.

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# The Eastern Seaboard Species of *Jardinella* (Mollusca, Gastropoda, Hydrobiidae), Queensland Rainforest-inhabiting Freshwater Snails Derived from the West

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ABSTRACT. Three species of the hydrobiid genus *Jardinella*, two of them new, are described from streams and rivers in north-east Queensland. Although associated with rainforests, these species appear to be derived from a western Queensland radiation of the genus.

PONDER, W.F., 1991. The eastern seaboard species of *Jardinella* (Mollusca, Gastropoda, Hydrobiidae), Queensland rainforest-inhabiting freshwater snails derived from the west. Records of the Australian Museum 43(3): 275–289.

Hydrobiid snails are well represented in south-eastern Australia but only one species, *Jardinella thaanumi* (Pilsbry), has been described from north-east Queensland. This species, the type of the genus *Jardinella* Iredale & Whitley, 1938, is found in streams and rivers on the eastern slopes of the Great Dividing Range. This paper provides information on the anatomy and distribution of *J. thaanumi* (Pilsbry) and two new species. Twelve additional species of *Jardinella* live in springs on the western side of the Great Dividing Range (Ponder & Clark, 1990).

## Materials and Methods

Most of the material on which this paper is based was collected in 1980 on a survey of the streams and rivers of the section of north-east Queensland between Townsville and the Daintree River.

Shells were measured by viewing the shells through a drawing apparatus located above a digitising-pad linked to a microcomputer. Selected parameters were digitised and the input converted to millimeters. The parameters measured were maximum shell length; maximum shell width, length of body whorl, length and width of aperture, diameter of umbilical chink, and diameter of protoconch. The convexity ratio (see Ponder *et al.*, 1989, for details), spire angle and the angle of the outer lip of the aperture were calculated by the computer from a series of points input via the digitising pad. The number of protoconch and teleoconch whorls were counted. All shell measurements were either at right angles or parallel to the longitudinal shell axis. Each measured individual was sexed.

The operculum was removed and the following

measurements taken:- maximum length, length of the white smear, and distance of the nucleus from the side opposite the growing end.

Four to five specimens from 12 populations were dissected and the pallial cavity and genital systems examined.

The heads of a few individuals were prepared by critical point drying and examined for ciliation patterns using a SEM. Radulae and opercula were mounted using standard methods for examination with the SEM.

Sex and species differences in shell and opercular measurements were tested for using t-Test. A discriminant function analysis was undertaken on shell and opercular measurement data using MDA in the BIOSTAT package (Pimentel & Smith, 1986).

Abbreviations used in this paper are as follows: AMS – Australian Museum, Sydney; ANSP – Academy of Natural Sciences of Philadelphia; QM – Queensland Museum, Brisbane. A table of measurements is given in the Appendix.

## Results

### Anatomy of *Jardinella thaanumi.* *External features.*

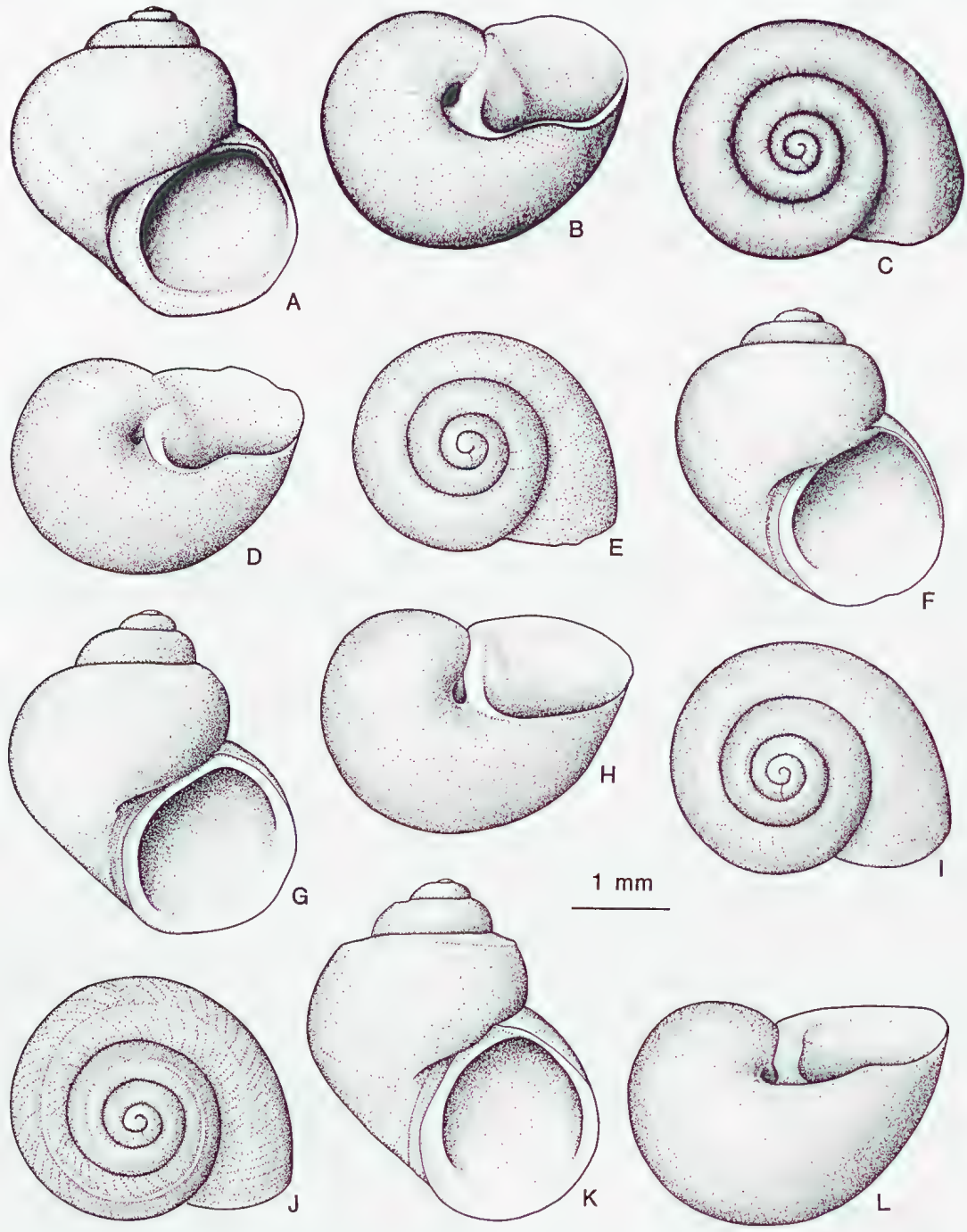


**Fig.1.** Shells of *Jardinella* species. A-F, *J. thaanumi* (Pilsbry); A-C, holotype (ANSP 77959a); D-F, subadult paratype (AMS C.8177). G-I, *J. tumorosa* n.sp., holotype. J-L, *J. tullyensis* n.sp., holotype.

The robust, trochoid shell (Figs 1-2) has a large aperture and a small umbilical chink and is yellow to brown in colour. The paucispiral operculum (Fig.3C) is yellow with a red to red-brown tinge, has an eccentric nucleus and is thin and flat. It usually bears on its inner surface a small white smear, sometimes with traces of two or three small, weak thickenings that suggest rudimentary pegs.

The snout is short, broad and rather indistinctly bilobed anteriorly (Fig.4, sn) with cilia scattered over its surface, especially laterally. The tapering cephalic tentacles (Fig.4, ct) are much longer than the snout in life and the well-developed eyes lie in distinct bulges at the bases of these tentacles. Each tentacle has a narrow midventral tract of cilia and there are scattered cilia over the ventral and dorsal surfaces (Fig.3D, E shows these features for one of the new species described below). The foot (Fig.4B, f) is short and broad with a broadly rounded posterior end and weakly developed anterior lateral lobes. An anterior pedal gland (Fig.4B, apg) is present but is not readily observed in the living animal. The sole of the foot is richly endowed with epithelial and subepithelial glands. The snout, proximal half of the tentacles and the dorsal side of the foot are usually pigmented with pale grey to black. The distal half of the tentacles are usually unpigmented except for a longitudinal narrow grey to black line mid-dorsally. Some specimens are unpigmented.

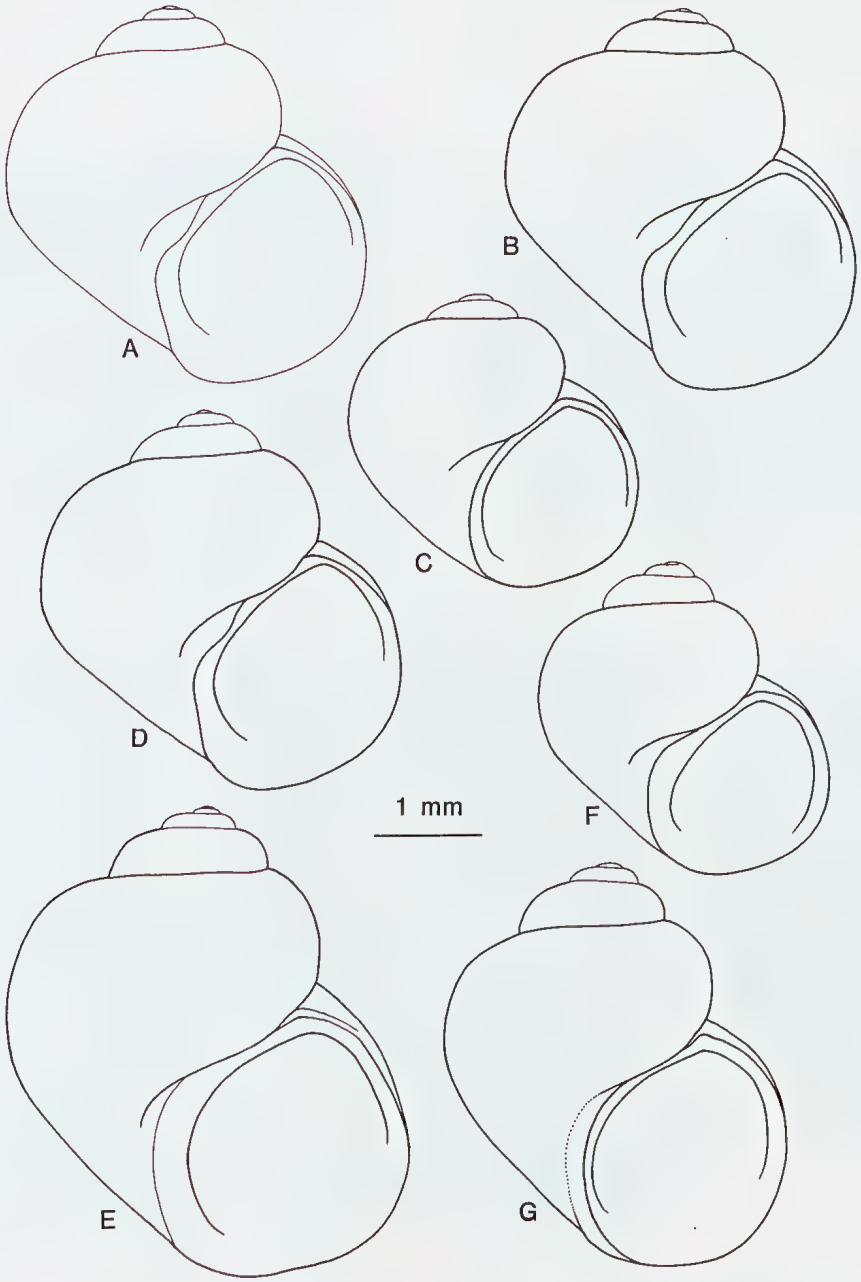


**Fig.2.** Shells of *Jardinella* species, showing some of the variation in size and shape. A-E, *J. thaanumi*, A-D, Barron Falls (AMS C.51466); E, Douglas Creek (AMS C.161649). F,G, *J. tumorosa* n.sp., paratypes (AMS C.161659).

*Pallial cavity.* The ctenidium extends for most of the length of the pallial cavity. It consists of 20-35 (average of material examined 27) triangular filaments that are shorter in height than they are wide. The osphradium is a narrow ridge which extends from about the middle of the ctenidium to a little before the posterior end. There is a well developed hypobranchial gland overlying the rectum in the posterior part of the pallial cavity.

*Alimentary canal.* A pair of well-developed jaws are present and in this respect and in the rest of the morphology of the anteriormost part of the alimentary canal, including the radula, it is typical of most other hydrobiids. The radula (Fig.5A-E) is described in detail below. The midoesophagus is rather broad as it passes through the nerve ring where it has long dorsal folds that are curled upwards and is conspicuously glandular ventrally. It becomes narrower behind the nerve ring and the ventral glandular epithelium is lost. The stomach is large, with the anterior and posterior chambers not particularly well differentiated. The stomach proper is about as high as it is long and has a single digestive gland opening. Internally the stomach contains a gastric shield and much of its surface is cuticularised. The style sac contains a crystalline style and ranges from about two thirds of the length of the stomach proper to slightly shorter. Sections of the digestive gland were unusual in that the gland did not contain large, conspicuous brown excretory spherules. Excretory cells are present, however, and their vacuoles contain tiny excretory granules.

The intestine is separated from the style sac, opening separately into the stomach. The intestine contains a large typhlosole and, as is normal in truncatelloideans, twists back along the style sac before running forward to the posterior pallial wall. The rectum enters the pallial cavity then immediately swings to the left and then to

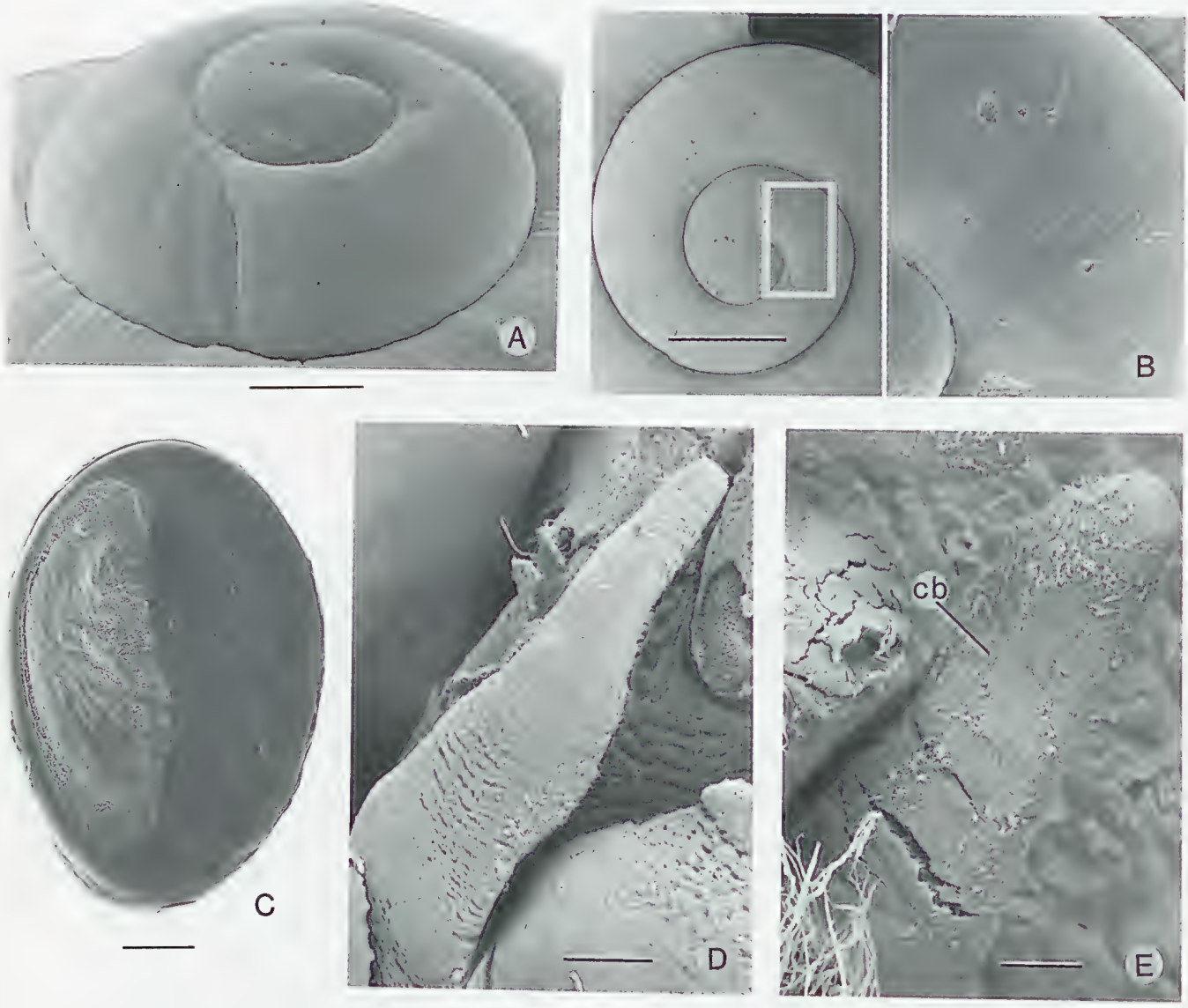


**Fig.3.** A-C, *Jardinella thaanumi* (Pilsbry). A,B, details of protoconch. Dowah Creek, Crystal Cascades, near Cairns. Area boxed in B magnified 4x on right. C, operculum. Douglas Creek on Palmerston Highway. D,E. *Jardinella tumorosa* n.sp., dorsal (D) and ventral (E) views of cephalic tentacles showing ciliation. Paratype. Scales:- A,D, 100 µm; B, 200 µm; C, 300 µm; E, 50 µm.

the right, thus forming a U-shaped loop across the posterior half of the pallial roof, before running along the right side of the anterior roof to terminate just inside the mantle collar where it forms a very short free papilla.

*Male genital system* (Fig.4A). The testis occupies the upper part of about one and a half whorls and consists of a single row of acini, the anterior part overlying the posterior chamber of the stomach. The convoluted seminal vesicle underlies the testis for about one third of a whorl behind the stomach.

The prostate gland is large, bean-shaped and approximately circular in section with approximately one half of the gland behind the posterior wall of the pallial cavity (in some specimens the prostate extends slightly more or slightly less than half of its length into the pallial wall). The very narrow, silvery pallial vas deferens emerges from the ventral side of the prostate gland at the point the gland enters the pallial cavity and runs ventrally along it until reaching the anterior end of the gland. Here it becomes convoluted, sometimes forming a small, tightly coiled ball at the anterior end of the prostate gland. From there it follows an undulating to convoluted path to the base of the penis. The penis (Fig.4A) lies behind the base of the right tentacle. It has a wide, transversely corrugated base (Fig.4A, pp) within which lies the narrow, convolute penial duct. In sections this duct is seen to be surrounded by a few muscle fibres and is lined with a very thin, ciliated epithelium. The basal and middle parts of the penis are lined with a thin, weakly pigmented, cuboidal epithelium which is covered with a thin cuticle. The unpigmented distal end of the penis (Fig.4A, dp) is narrow, tapering and smooth, the penial aperture very minute and terminal. This part of the penis is not cuticularised and the cuboidal to short columnar epithelium contains numerous non-staining (mucus?) gland cells.

*Female genital system* (Fig.6A). The ovary is a little shorter than the testis and the narrow, thin-walled upper oviduct runs across the lower right side of the stomach to open to the coiled oviduct just behind the posterior pallial wall. The coiled oviduct (co) lies against the left (inner) side of the albumen gland (ag) and forms a U-shaped loop before doubling back to run just below and parallel to the bursal duct (bd), these two ducts joining at the posterior pallial wall (pw) to form a very short common duct which almost immediately opens to the ventral channel (vc) of the capsule gland. The coiled oviduct is lined with a ciliated, short columnar epithelium. The bursa copulatrix (bc) is an ovoid sac located behind the albumen gland and is lined with large, irregular columnar cells with granular cytoplasm and proximal nuclei. Its rather wide duct

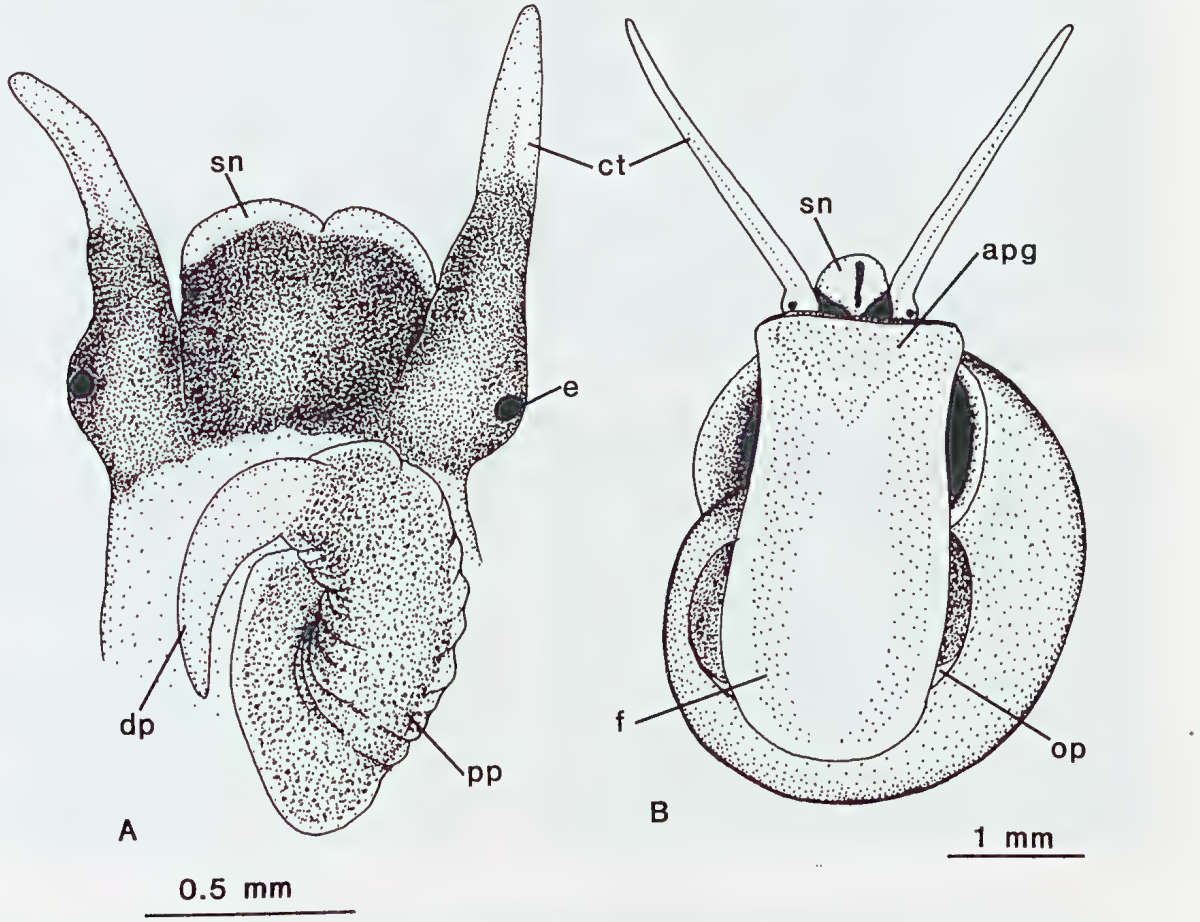


**Fig.4.** Head and foot of *Jardinella thaanumi* (Pilsbry). A, dorsal view of head and penis, from living material; Douglas Creek. B, ventral view of living animal, Barron River Gorge. apg – anterior pedal gland; ct – cephalic tentacle; dp – distal part of penis; e – eye; f – foot; op – operculum; pp – proximal (basal) part of penis; sn – snout.

emerges from about the middle of the anterior side of the bursa. Internally the ciliated columnar epithelium lining the duct is thrown into longitudinal ridges. The bursal duct and, to a lesser extent, the coiled oviduct, is surrounded by a layer of muscle fibres. The seminal receptacle (sr) opens by way of a short duct to the coiled oviduct near the posterior end of the last section of the coiled oviduct just as it begins to run parallel with the bursal duct.

The ventral channel is unusual in that it is lined with a thick columnar epithelium containing mucous cells. The longitudinal fold in the ventral channel is large and thick. The small but distinct genital opening is set back approximately one third of the length of the gland from its anterior end. There is no swollen anterior vestibule like that seen in some western members of the genus.

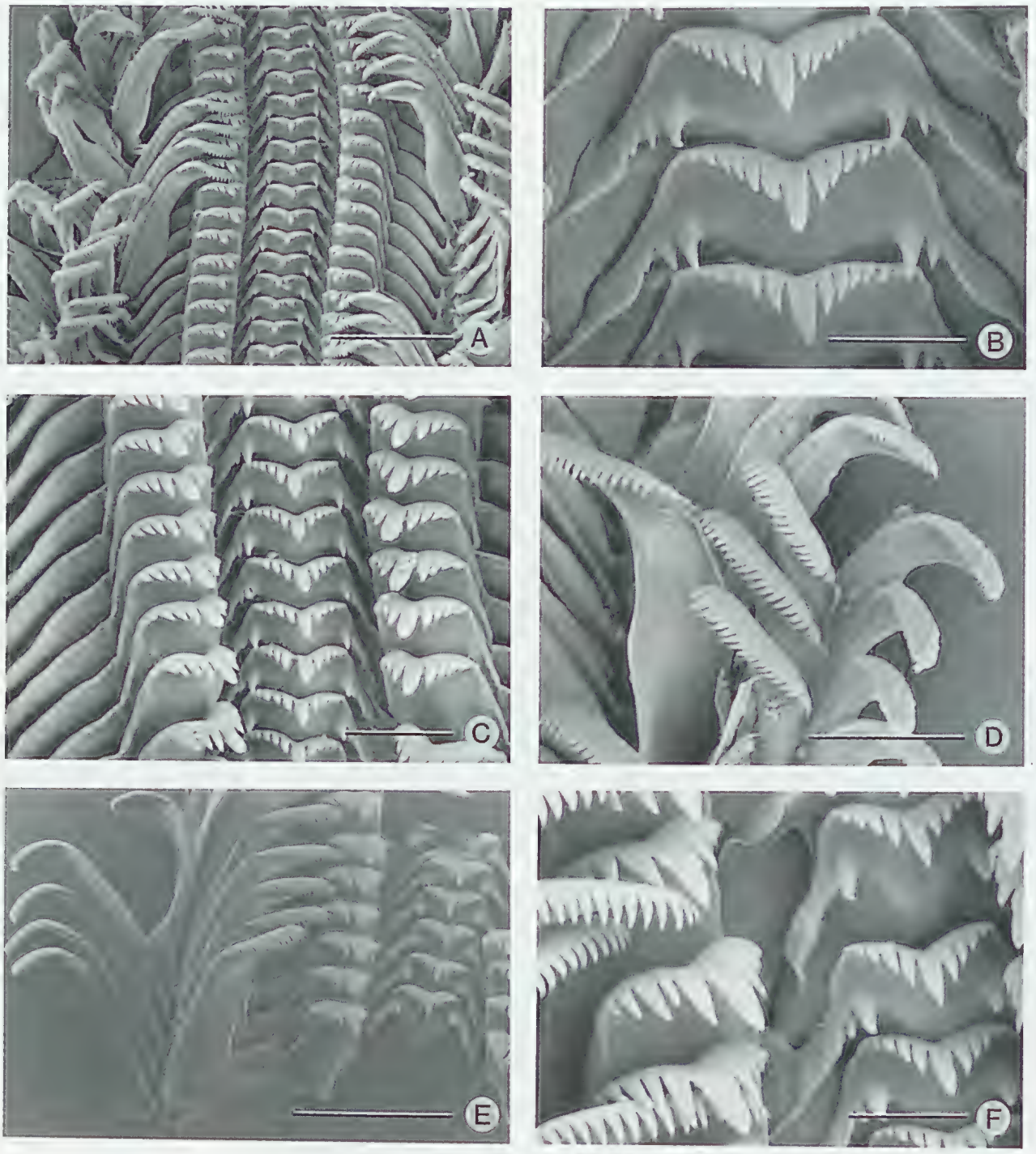


**Fig.5.** Radulae of species of *Jardinella*. A-E, *J. thaanumi*, A, middle part of ribbon showing all teeth; B, detail of central teeth; C, detail of central and lateral teeth; D, detail of marginal teeth; E, teeth on one side of radula showing detail of bases of central and lateral teeth. A-D, Barron River Gorge; E, Douglas Creek. F, *J. tumorosa* n.sp., showing central, lateral and part of inner marginal teeth; paratype. Scales:- A, 50 µm; B,F, 10 µm; C,D, 20 µm; E, 30 µm.

The orange-red capsule gland is approximately twice as long as it is wide. It terminates at the posterior pallial wall where it joins with the smaller albumen gland.

*Nervous system.* The cerebral ganglia are connected by a rather long commissure, located at the posterior end of the ganglia, which is about as long as the ganglia are wide. The pleural ganglia abut the cerebral ganglia. The supraoesophageal - pleural connective is variable in length. In the specimens dissected it varies from about equal to the length of the supraoesophageal

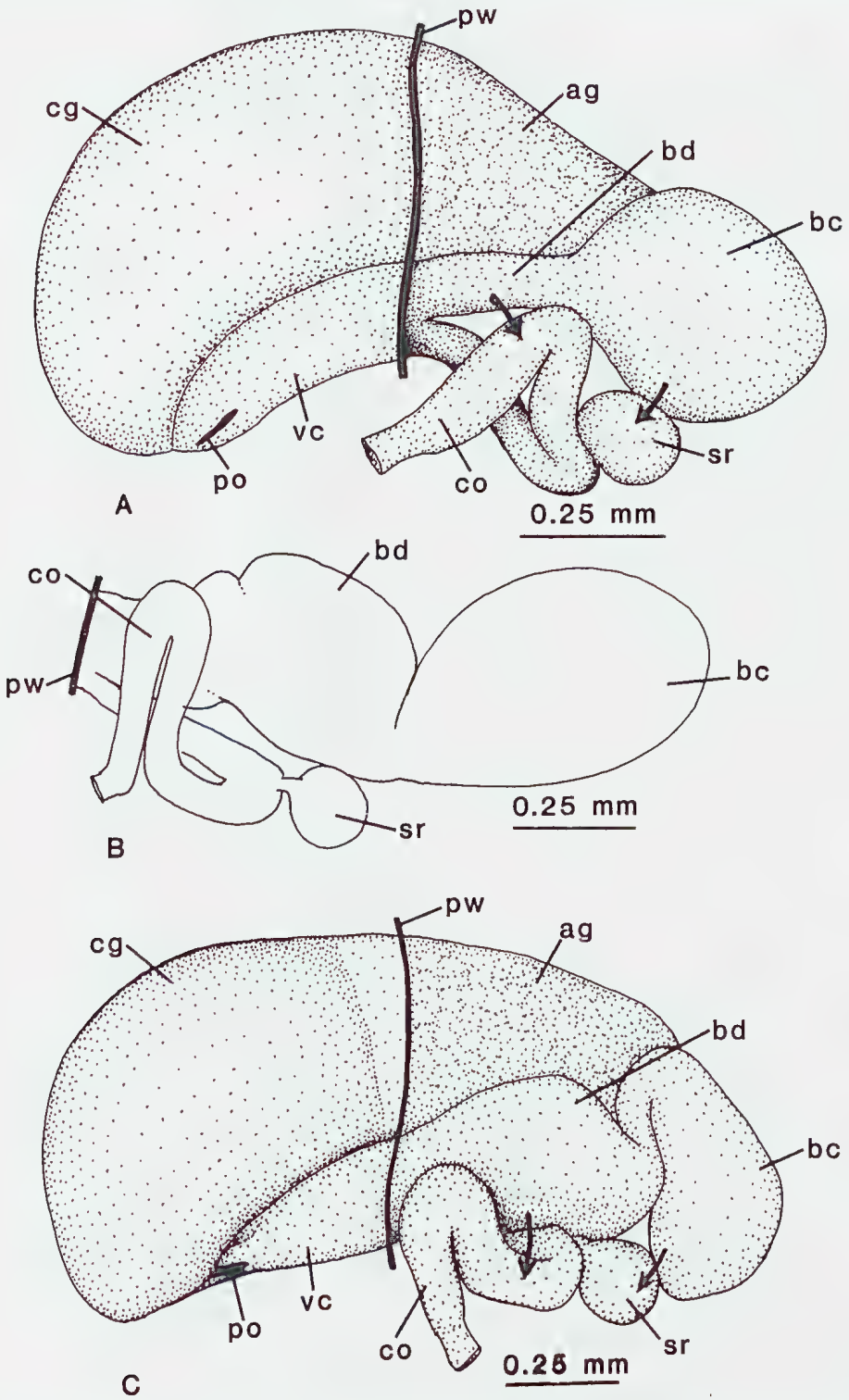


**Fig.6.** Female genital ducts of species of *Jardinella*, viewed from the left side. A, *J. thaanumi* (Pilsbry), Barron River (Stn 45b). B,C, *J. tumorosa* n.sp., B, coiled oviduct, bursa copulatrix and its duct; Pine Creek (Stn 44); C, paratype. The arrows indicate the directions in which parts of the genitalia have been moved. ag – albumen gland; bc – bursa copulatrix; bd – bursal duct; cg – capsule gland; co – coiled oviduct; po – pallial opening of oviduct; pw – posterior wall of pallial cavity; sr – seminal receptacle; vc – ventral channel.

ganglion to about twice the length of the ganglion. The suboesophageal ganglion is connected to the left pleural ganglion by a very short connective. The ovoid pedal ganglia abut one another and each has a small propodial ganglion anteriorly attached by a short connective. There is a statocyst, which contains a single statolith, at the posterior end of each pedal ganglion.

*Reno-pericardial system.* The renal organ is thin-walled except for a thin renal gland on the outer wall. This gland is more than twice as wide as it is long and is orientated with its anterior edge along the posterior pallial wall. Neither the renal organ nor the small pericardium protrude into the pallial roof. A short, narrow, reno-pericardial duct is present.

**Remarks.** This species is considered to be congeneric with the western Queensland species assigned to the genus by Ponder & Clark (1990) because it has the following diagnostic characters: a) the operculum lacks pegs but usually has a white smear on its inner surface; b) the radula has two pairs of cusps on the base of each of the central teeth; c) the penis has the distal portion smooth and differentiated from the rest of the penis, and d) the pallial vas deferens is convoluted.

The robust, trochiform shell with its rather large aperture and short spire is a shell shape well adapted to life in rivers. Similar shell forms are seen in other river-living hydrobiids such as *Beddomeia* and *Posticobia* in Australia, the northern hemisphere Lithoglyphinae (*Lithoglypus* in Europe, *Gilla*, *Somatogyrus*, etc. in North America), as well as the South American *Potamolithus*.

Individuals of *J. thaanumi* from several localities were parasitised by trematodes.

## Taxonomy

## Hydrobiidae

### *Jardinella* Iredale & Whitley

*Jardinella* Iredale & Whitley, 1938: 67.

**Type species.** *Petterdiana thaanumi* Pilsbry, 1900 by original designation.

**Diagnosis.** The genus has been diagnosed and discussed by Ponder & Clark (1990). All three species described below form a distinct group which can be separated from the western members of the genus by the following combination of characters. Shell trochiform, of medium to large size (up to about 4 mm in length), smooth, or with keeled shoulder, with umbilical chink or narrow umbilicus. Penis with long, tapering, non-pigmented distal portion. Pallial oviduct with narrow vestibule, pallial opening at about one third length of capsule gland.

### *Jardinella thaanumi* (Pilsbry)

*Petterdiana Thaanumi* Pilsbry, 1900: 144.–Hedley, 1901: 727, pl.48, fig.11.

*Jardinella thaanumi*.–Iredale & Whitley, 1938: 67.–Iredale, 1943: 203.

**Type material.** HOLOTYPE and PARATYPES: near Cairns, Queensland; type locality restricted to Barron River herein. LECTOTYPE (ANSP, 77959A, selected herein, and 12 PARALECTOTYPES, ANSP, 77959; 2 PARALECTOTYPES AMS, C.8177).

**Additional material examined** (an asterisk indicates material has been examined anatomically): Barron Falls, near Cairns, 16°51'20"S 145°38'50"E, coll. C. Hedley, AMS C.9301; Barron Falls, near Cairns, 16°51'20"S 145°38'50"E, coll. C. Hedley, AMS C.51466; Barron Falls, near Cairns, 16°51'20"S 145°38'50"E, 15 June 1926, coll. T. Iredale & G.P. Whitley, AMS C.161641; Barron River, near Cairns, 16°51'20"S 145°38'50"E, coll. Sgt. B. Shipway AMS C.161642; *Barron River Gorge, near Cairns, 16°51'20"S 145°38'50"E, near bridge, 1 Dec. 1982, coll. I. Loch, AMS C.161643; Cairns district, 16°55'S 145°46'E, 1890-91, coll. C.J. Wild, AMS C.161644; *Dowah Creek, Crystal Cascades, near Cairns, 16°57'45"S 145°40'50"E, 14 Oct. 1981, coll. W.F. Ponder & I. Loch, AMS C.161645; off Palmerston Highway, near Innisfail, 17°32'S 146°01'E, in Goolagong Creek, on stones and leaves, 10 June 1973, coll. I. Loch, AMS C.161666; rapids below Lake Placid, near Cairns, 16°51'20"S 145°38'50"E, lower end of Barron Gorge, 2 Jan. 1959, coll. D. McAlpine, AMS C.161647; Rocky Creek, Atherton, 17°16'S 145°29'E, coll. F. Allen, AMS C.161648; *Fishers Creek, Palmerston Highway, 17°34'20"S 145°53'40"E, tributary of North Johnstone River, in stony creek, amongst leaves and stones in shallow water, 28 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 24), AMS C.161661; *Douglas Creek, at Palmerston Highway, 17°35'55"S 145°43'25"E, 8.6 km south-east from Beatrice River crossing, in small boulder creek, on leaves and stones, 28 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 25), AMS C.161649; Barron River, Hypipamee Crater, 17°25'45"S 145°29'50"E, south-east of Herberton in 'The Crater National Park', on stones and leaves, in small creek next to lookout carpark, 29 Sept. 1980, coll. W. F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 28), AMS C.161663; *Dinner Falls, Barron River, Hypipamee Crater, 17°25'45"S 145°29'50"E, in pools, along sides and in shallow water - rocky and sandy area, none on actual falls, 29 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 28a), AMS C.161662; *Wright Creek, Lake Eacham, 17°16'55"S 145°38'55"E, tributary of Barron River, Lake Eacham National Park, on stones, leaves etc., in swift creek with solid rock bed, also in feeder creek near bridge on Lake Eacham - Gordonvale Road, 29 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 33), AMS C.161660; *Freshwater Creek, below intake, west of Cairns, 16°58'00"S 145°40'30"E, in quiet corners of side creek, swift flow on rock bed, 30 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 41), AMS C.161650; *Dowah Creek, at Freshwater Creek junction, west of Cairns, 16°57'45"S 145°40'50"E, on stones and leaves in pools, 30 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 42), AMS C.161651; Barron River, at Barron Gorge Power Station, 16°59'45"S 145°50'20"E, in small creek on south-west

side of gorge near power station, amongst leaves in steep creek and falls, 30 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 45a), AMS C.161664; *Barron River at Barron Gorge Power Station, 16°51'20"S 145°38'50"E, in main gorge, in rocky river bed, in piles of stones behind boulders in swifter flow, 30 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 45b), AMS C.161652, Barron River Gorge, 16°52'S 145°47'E, halfway to hydro station, in river, 7 Oct. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 66), AMS C.161665; ?Bellenden Ker Range, 17°12'S 145°51'E, coll. J. Brazier, AMS C.7460.

**Diagnosis.** Shell with umbilicus closed (umbilical chink only) or very narrowly open in adults; shoulder slightly flattened to convex. Bursal duct parallel sided. Renal gland wider than long and lies behind pallial wall.

**Description.** *Shell* (Figs 1A-F, 2A-E). Trochiform, 2.70-4.03 mm in length [mean 3.43 (M), 3.69 (F)]; 2.64-3.82 mm in width [mean 3.15 (M), 3.46 (F)]; sexually dimorphic in total width and aperture width (*P* less than 0.05); of medium thickness, semi-opaque, with indistinct, transparent periostracum. Spire angle 74.3-86.6° [mean 80.15 (M), 80.49 (F)]. Protoconch (Fig.3A,B) of about 1.20-1.35 whorls. Teleoconch of 2.75-3.05 convex whorls [mean 2.89 (M), 2.96 (F)]. Convexity ratio 0.20-0.26 (mean 0.23 in both sexes); shoulder convex to slightly flattened. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.57-0.70 [mean 0.65 (M), 0.64 (F)]. Inner lip slightly thickened forming distinct shelf across part of, to most of, lower part of umbilical chink. Outer lip simple, prosocline, angle 30.03-40.42° [mean 35.13 (M), 34.58 (F)]. Width of umbilical chink 0.18-0.46 [mean 0.28 (M), 0.33 (F)], umbilicus narrow and open in juveniles, usually closed in adults. Colour white or yellow-white to pale pink-brown or yellow-brown.

*Shell dimensions*. See Appendix.

*Operculum* (Fig.3C). Operculum thin, pale yellow with red patch to uniform red; 1.38-1.96 mm in length [mean 1.69 (M), 1.79 (F)]. With or without white smear up to 0.82 mm in length [mean 0.51 (M), 0.44 (F)]. Ratio of operculum length to position of nucleus 2.8-3.9 [mean 3.60 (M), 3.45 (F)].

*Radula* (Fig.5A-E). Central teeth each with 4-7 pointed lateral cusps; central cusp pointed, about twice as long as adjacent cusps; 2 pairs of basal denticles, outermost pair smaller than inner pair, very minute third pair in some specimens; dorsal edge concave; basal process narrow, U-shaped. Lateral teeth with cusp formula 3-1-(4-6); primary cusp up to twice as long as adjacent cusps, with rounded distal end, other cusps pointed; with small but distinct basal bulge; outer shaft about twice as long as cutting edge. Inner and outer marginal teeth with many small, sharp cusps restricted to distal end of teeth, those on inner marginal larger than on outer.

*Head-foot* (Fig.4). Cephalic tentacles subtriangular in section, with no dorsal ciliated bands present; midventral ciliated band along most of ventral surface. Snout dark grey to black; anterior end unpigmented; dorsal sides of cephalic tentacles pale to dark grey; sides of foot and opercular lobe pale to dark grey. Visceral coil pigmentation mostly black or dark grey.

**Anatomy.** *Mantle cavity*. Ctenidium with ctenidial apex on right, with 20-35 (n=27; average 27) triangular filaments shorter in height than wide. Free left edge of longest filaments 0.16-0.47 mm long (preserved material, n=22; average 0.29). Osphradium between posterior end and middle of ctendium. Hypobranchial gland well developed. No glandular pad to left of ctendium, or near anus. Rectum with well-developed U-shaped arch in males, less obvious in mature females; anus near mantle edge. Kidney not extending forward into mantle roof.

*Male genital system*. Penis (Fig.4A) with lobes absent; distal end of penis tapering; unpigmented. Vas deferens with several loops/coils.

*Female genital system* (Fig.6A). Pallial oviduct with ventral channel wide posteriorly and narrow anteriorly. Pallial opening at about one third length of capsule gland from anterior end. Seminal receptacle lies at anterior edge of bursa. Bursal duct not swollen, arises from middle of anterior side of bursa. Coiled oviduct and bursal duct separate to posterior mantle wall. Coiled oviduct simple U-shape. Rudimentary penis absent in females.

*Egg capsules*. Transparent, lens-shaped, 0.48-0.53 mm (mean 0.50 mm, n=6) in diameter, laid singly in umbilical chink of females (Stn 25 only).

**Remarks.** The type locality of this species is "near Cairns". The types can be matched with shells from the Barron River and its tributaries and the type locality is here restricted to that river. In shell measurements, including spire angle and aperture angle (Fig.8), the three adults in the type series fall within others attributed to *J. thaanumi*. These specimens have the key characters of *J. thaanumi* in possessing a very narrow to closed umbilicus and the inner lip forms a shelf over the umbilical chink. In addition the shoulder in several specimens in the type series is slightly flattened, a character rarely observed in *J. tumorosa*. The subadult (Fig.1D-F) and juvenile specimens have a very narrow umbilicus, a character typical of *J. thaanumi*. One specimen, segregated as the "holotype", is selected as the lectotype because no reference was made of a holotype in the original description and there has not been a subsequent designation of a lectotype.

The specimen figured by Hedley (1901) is typical of large forms of this species. The locality is given as Bellenden Ker Range, which would place it in the headwaters of the Mulgrave River, the location of the species described below. To date no populations are known from the Mulgrave River or its tributaries that have this shell morphology and it is likely that these specimens (AMS, C.7460), which originated from John Brazier, are mislocalised.

There is considerable variation both within and

between populations but, unfortunately the available material does not allow a proper analysis of this variation. Some populations (e.g., Freshwater Creek, Stn 41) are small, others much larger (e.g., Douglas Creek, Stn 25). Some of this interpopulation variation is expressed in the differences in the means for the major shell dimensions (Appendix) and the intrapopulation variation in the standard deviations.

This species is apparently confined to the Barron and Johnstone River systems, both of which flow from the Atherton Tablelands, the Barron River flowing north-east and the Johnstone River flowing south-east. One lot (shells only) in the Australian Museum labelled Port Douglas (C.161646, coll. C.J. Wild, Aug. 1891) may be mislocalised because a number of localities were examined around Port Douglas (see Fig.7) without success. There is, however, an unconfirmed report of a *Jardinella*-like snail from the Bloomfield River, near the Bloomfield River Mission, just north of the Daintree River, Cape York Peninsula (V. Kessner, personal communication).

### *Jardinella tumorosa* n.sp.

**Material examined.** HOLOTYPE and PARATYPES: Mulgrave River, at Mulgrave River Forestry Road, 17°14'20"S 145°46'25"E, in small tributary on east side of river, 29

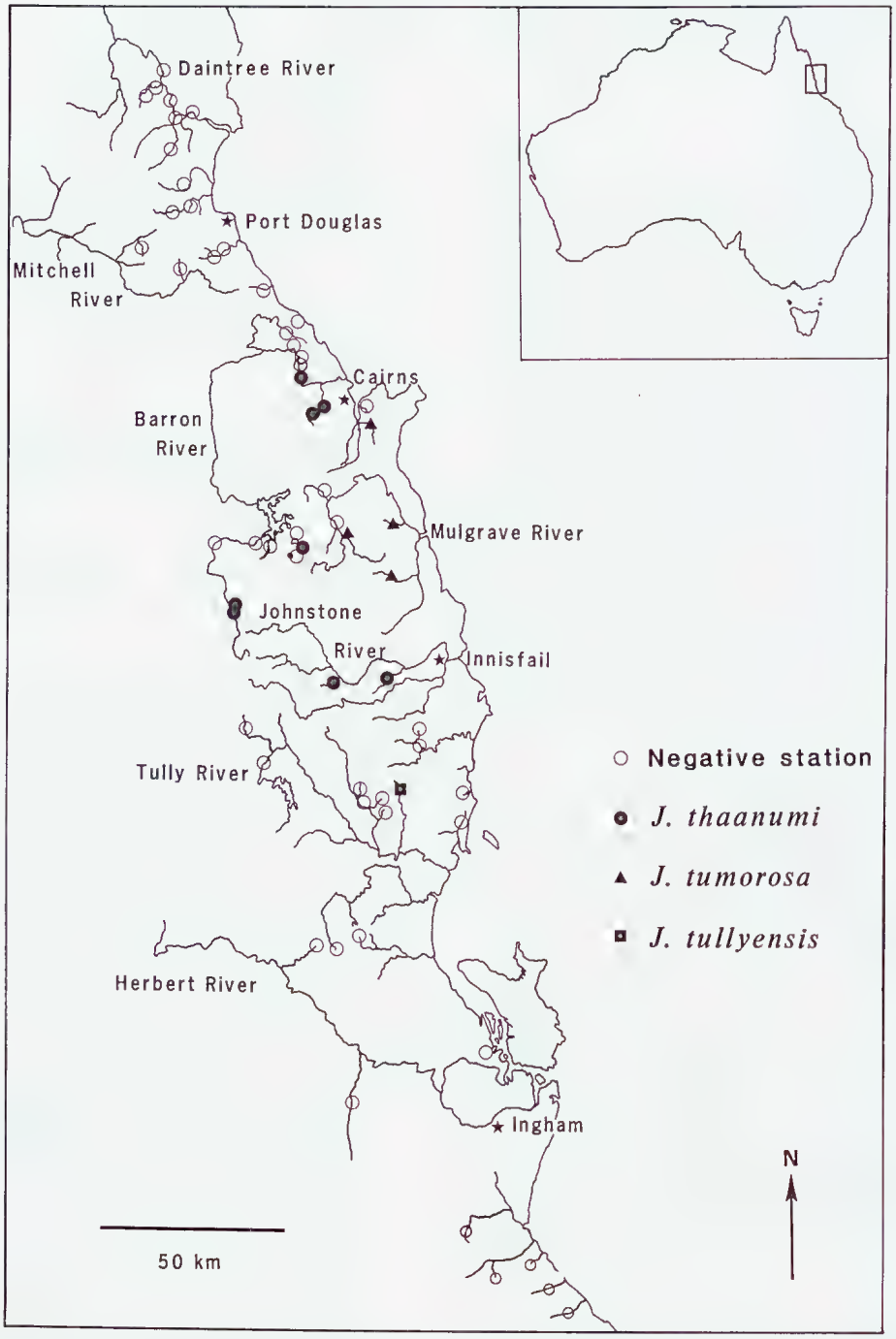


**Fig.7.** Distribution map of the species of *Jardinella*. The open circles indicate negative sites specifically searched for *Jardinella*.

Sept. 1980, coll. W.F. Ponder, I. Loch, H .& E. Vokes & J. Stanisic (Stn 36).

HOLOTYPE – Stn 3, AMS C.161655. PARATYPES, 90 – Stn 36, AMS C.161659 (73); AMS C.161667 (13); QM MO24080 (4).

**Additional material examined.** Little Mulgrave River, on Mareeba - Cairns Road, 17°08'10"S 145°42'45"E, at bridge just before junction with Big Mulgrave, 18 Oct. 1975, coll. P.H. Colman, AMS C.161653; Fishery Falls, Fishery Creek, south of Cairns, 17°11'35"S 145°52'40"E, tributary of lower part of Mulgrave River, 29 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 38), AMS C.161656; The Boulders, west of Babinda, 17°20'40"S 145°52'20"E, east of Bartle Frere in wide, swift stream, 29 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 40), AMS C.161668; Pine Creek, north-west end of Malbon Thompson Range, north-west of Little Mulgrave River, 16°59'45"S 145°50'20"E, stony creek with sluggish flow about 1 km east of Yarrabah Road, 30 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 44), AMS C.161654.

Specimens from all populations examined anatomically.

**Diagnosis.** Shell with narrow, open umbilicus in adults; shoulder convex or (rarely) slightly flattened. Bursal duct swollen; renal gland narrower than long and protruding for about one third of its length into posterior pallial roof.

**Description.** *Shell* (Figs 1G-I, 2F,G). Trochiform, 2.80-3.74 mm in length [mean 3.22 (M), 3.19 (F)]; 2.59-3.23 mm in width (mean 2.90 in both sexes); not sexually dimorphic in size (*P* greater than 0.05 for all measured shell characters); of medium thickness, semi-opaque, with indistinct, transparent periostracum. Spire angle 73.01°-82.44° [mean 77.07 (M), 77.85 (F)]. Protoconch of 1.25-1.35 whorls. Teleoconch of 2.75-3.10 convex whorls [mean 2.98 (M), 2.95 (F)]. Convexity ratio 0.19-0.27 [mean 0.22 (M), 0.23 (F)]; shoulder convex or, rarely, slightly flattened. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.56-0.65 [mean 0.63 (M), 0.60 (F)]. Inner lip lightly to moderately thickened, forming a narrow reflection across lower umbilical chink in some specimens but lacking distinct shelf seen in *J. thaanumi*. Outer lip simple, prosocline, angle 21.64-29.51° [mean 24.72 (M), 26.89 (F)]. Umbilical chink 0.21-0.37 mm in width [mean 0.25 (M), 0.28 (F)], umbilicus narrowly open. Colour pale pink-brown.

*Shell dimensions.* See Appendix.

*Operculum.* Operculum thin, pale yellow, usually also with red colouration; 1.18-1.78 mm in length [mean 1.64 (M), 1.58 (F)]. With or without white smear up to 0.74 mm in length [mean 0.45 (M), 0.48 (F)]. Ratio of operculum length to position of nucleus 2.79-3.44 [mean 3.11 (M), 3.15 (F)].

*Radula* (Fig.5F). Similar to that of *J. thaanumi*; differing in tending to have smaller numbers of cusps on central and lateral teeth [central teeth formula (4-5)-1-(4-5); lateral teeth (3-4)-1-(4-5)] and primary cusp on lateral teeth pointed.

*Head-foot.* As in *J. thaanumi*; pigmentation lacking

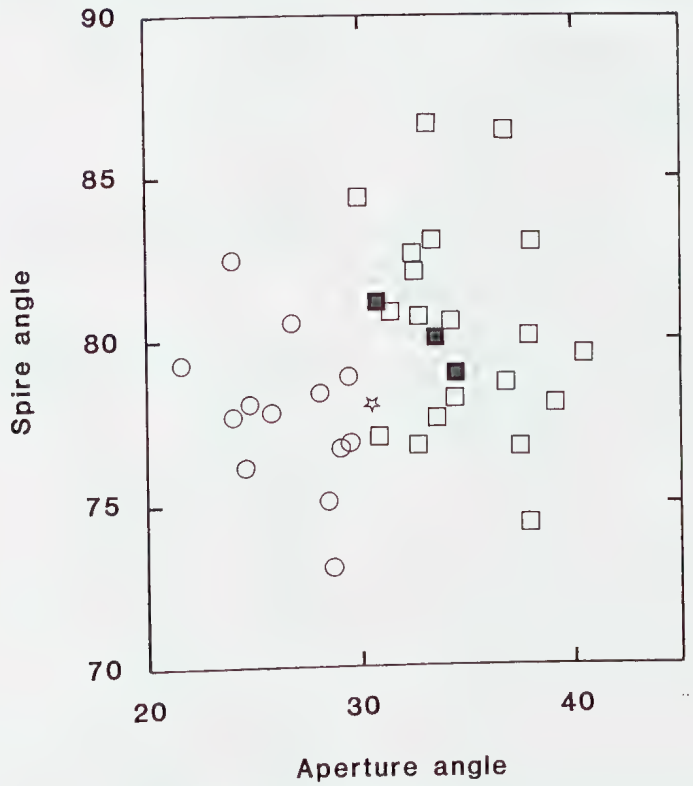


**Fig.8.** Plot of aperture angle against spire angle for specimens of *Jardinella* at terminal growth. Open squares – *J. thaanumi* (closed squares are the three adults in the type series); circles – *J. tumorosa*; star – *J. tullyensis* (holotype).

in some specimens. Tentacle ciliation (Fig.3D,E) as in *J. thaanumi*.

**Anatomy.** As in *J. thaanumi* except for following characters: ctenidium filaments 25-33 (n=8; average 28.8), left free edge of longest filaments 0.23-0.41 mm in length (n=8; average 0.28 mm). Bursal duct (Fig.6B,C, bd) extremely expanded (balloon-like) and displacing much of albumen gland. Bursal duct typically enters bursa at dorsal anterior corner of bursa (not middle of anterior face as in *J. thaanumi*) (see note about Stn 44 below). Renal gland longer than wide; anterior third, together with anterior part of renal organ, in posterior pallial roof.

*Egg capsules.* Unknown.

**Remarks.** The shell of this species is virtually identical to *J. thaanumi* but, unlike most adult specimens of that species, it has an open umbilicus. The shape of the bursal duct, however, is a readily discernible character that can be used to separate females of the two species, *J. tumorosa* having a swollen bursal duct whereas that of *J. thaanumi* is parallel-sided. This character was consistent in all five populations of *J. tumorosa* and was apparent even in submature females. The bursal duct in all populations examined of *J. thaanumi* was also consistent for that species. Specimens of *J. tumorosa* from Stn 44 (outside the Mulgrave River catchment) had a similar, swollen bursal duct to that of typical specimens but differed in that the bursal duct joined the bursa in the middle to lower part of its anterior edge (Fig.6B) rather than the upper part of the anterior edge. The ctenidial filament count of *J. tumorosa* corresponds to the high part of the range for *J. thaanumi* with a correspondingly higher average than for all of the *J. thaanumi* populations summed. The renal organ also differs markedly in the two species – it does not penetrate the pallial roof and the long axis of the renal gland is orientated across the coiling axis of the animal in *J. thaanumi* (parallel to the posterior pallial wall) whereas the opposite situation is seen in *J. tumorosa*. The radula also differs in tending to have a smaller number of cusps on the central and lateral teeth and in the primary cusp on the lateral teeth being pointed, not rounded, distally. Despite these differences the overall similarity with *J. thaanumi* suggests a relatively recent divergence of these taxa.

This species lives in a coastal wedge in the middle of the range of *J. thaanumi*. It is confined to the Mulgrave River which drains the highest mountains in Queensland, Bellenden Ker and Bartle Frere. These mountains are residual features of considerable age, being composed of Permian granitoids (Henderson & Stephenson, 1980).

As noted above the shells of *J. thaanumi* and *J. tumorosa* are very similar. Comparisons of the two species (three populations of *J. thaanumi* and two of *J. tumorosa* pooled) show that several variables are significantly different (*P* less than 0.05). These include shell length, shell width, aperture length, aperture width, length of body whorl and the length of the white smear on the operculum – these all reflecting the generally larger size of two of the populations of *J. thaanumi*. Other characters are not size related – these including the angle of the outer lip of the aperture (larger in *J. thaanumi*), the spire angle (larger in *J. tumorosa*) and the number of protoconch whorls (slightly larger in *J. tumorosa*). The number of teleoconch whorls is not significantly different but when plotted against a size related variable such as shell length or shell width the two species are reasonably well separated. A good separation is obtained by plotting spire angle against aperture angle (Fig.8). Discriminant function analysis using shell and opercular measurement data also separates the two species, although there is some overlap. The extent of overlap is reduced by removing the variables which show almost no differences (convexity, umbilical chink width, opercular length and opercular nucleus) from the data set.

**Etymology.** *Tumorosus* (Latin), bloated, inflated, referring to the diagnostic swollen bursal duct.

### *Jardinella tullyensis* n.sp.

**Material examined.** HOLOTYPE and PARATYPES: Boulder Creek, north of Tully, 17°53'10"S 145°55'20"E, tributary of Bluegum Creek, tributary of Banyan Creek, tributary of Tully River, under stones and leaves on sides of stream, 28 Sept. 1980, coll. W.F. Ponder, I. Loch, H. & E. Vokes & J. Stanisic (Stn 21). HOLOTYPE – AMS C.161657. PARATYPES, 3 – AMS C. 161658 (2); QM MO24081 (1).

**Diagnosis.** Shell with narrow, open umbilicus; shoulder flat, narrow, separated from rest of shell by sharp angulation. Bursal duct unknown. Renal gland narrower than long and protruding for about one third of its length into posterior pallial roof.

**Description.** *Shell* (Fig.1J-L). Trochiform, 3.51 mm in length; 3.09 mm in width; rather thin, semitransparent, with indistinct, transparent periostracum. Spire angle 78°. Protoconch of about 1.25 whorls. Teleoconch of 3 convex whorls; convexity ratio 0.26; shoulder flat, separated from rest of whorl by sharp angulation. Teleoconch sculpture of faint, prosocline growth lines. Aperture length/shell length ratio 0.60. Inner lip well developed, forming a narrow shelf across lower part of umbilicus. Outer lip simple, prosocline, angle 30.5°. Umbilical chink 0.33 mm in width, umbilicus open, narrow.

*Dimensions of holotype.* See Appendix.

*Operculum.* Operculum thin, pale yellow, with some red colouration; 1.76 mm in length; with white smear 0.59 mm in length. Ratio of operculum length to position of nucleus 3.2.

*Radula.* Not examined.

*Head-foot.* Similar to *J. thaanumi* but lacking pigment.

**Anatomy.** (Holotype and two subadults examined). Similar to type species. Ctenidium within large end of range for *J. thaanumi*, holotype with 35 filaments and largest filaments 0.47 mm along free right edge (cf. 0.16-0.47 mm in *J. thaanumi* and 0.23-0.41 mm in *J. tumorosa*). Subadults with 30 filaments and 0.23-0.25 mm long on left free edge. Genital system (both male and female) immature in available material. Renal gland longer than wide, renal organ protrudes into mantle roof for about half length of renal gland.

**Remarks.** This species is differentiated because of the distinctly shouldered shell which is present in all specimens in the sample. None of the other specimens of *Jardinella* examined have developed this character, although some weak shouldering is present in some material of *J. thaanumi*. The unpigmented head-foot occurs in some specimens/populations of both *J. thaanumi* and *J. tumorosa*. The ctenidium of the one adult is larger than in the other two species. It has more filaments than any of the examined material of *J. tumorosa* and is equalled in this regard by only one population of *J. thaanumi* (Stn 25) but these have narrower filaments (0.31-0.39 mm). Two specimens of *J. thaanumi* examined from Stn 33 however, have filaments 0.47 mm wide but have fewer (28) filaments. The next longest filaments seen in *J. thaanumi* are those in Stn 25 (see above).

This taxon is known from only one adult (has a mature shell aperture, even if reproductively immature) and a few immature specimens collected in a small rainforest stream. It will, no doubt, be found in additional localities associated with the Tully River.

**Etymology.** Named for Tully, the town nearby the collecting site and the name of the river into which Boulder Creek flows.

## Discussion

*Jardinella thaanumi* has been thought (Pilsbry, 1900; Hedley, 1901) to be a relative of the Tasmanian *Beddomeia* group, which forms a separate radiation from the rest of the Australian Hydrobiidae (Ponder, 1991). Iredale (1943), however, suggested that it may not be related to the Tasmanian genera. These snails are distinguished by their typically low-spired shells (like *Jardinella*), the lack of a white smear or pegs on the inner surface of the operculum and the possession of a single pair of cusps on the base of each central tooth of the radula. *Jardinella* belongs to the main hydrobiid radiation in Australia which is typified by the genus *Fluvidona*. This group typically has a conical or pupoid shell, an operculum bearing a white smear and/or pegs and the radula has more than one pair of cusps on the base of each central tooth.

Anatomically *Jardinella* is a typical member of the Hydrobiidae, the only unusual feature being the conspicuously glandular ventral lining of the midoesophagus that appears to be similar histologically to the tissue seen in an oesophageal gland. Most hydrobiids do not possess such glandular tissue although I have seen it in a poorly developed state in some other Australian hydrobiids.

The discovery of hydrobiids in western Queensland which are apparently congeneric with the coastal species of *Jardinella* has recently been reported (Ponder & Clark, 1990). A cladogram was produced by Ponder & Clark (1990) showing the relationships of the western Queensland species to *J. thaanumi* (based on data provided in this paper) and that species was included in the same subgroup as the more derived members of the radiation from the eastern part of western Queensland. This analysis suggests that the coastal species of *Jardinella* were derived from the western radiation. The location of the most plesiomorphic members of that radiation in springs in the western and south-western parts of Queensland suggests that this radiation commenced in the west and moved eastwards.

The apparent western derivation of the eastern species of *Jardinella* appears to be in contrast to the normally accepted idea that rainforest faunas are relictual. If a western origin occurred in the Pliocene or later, this would suggest that the genus diversified in an arid to semi-arid environment in permanent (mainly artesian) springs (Ponder & Clark, 1990). It is unlikely, given the pattern of anatomical diversification in the present western fauna, that the eastern fauna was derived from the west as early as the Miocene when a continuous rainforest habitat may have been available. However, wet periods during the Pliocene and Pleistocene would probably have provided corridors of semi-continuous freshwater habitat through the Great Dividing Range. A species of *Jardinella* is known from Carnarvon Gorge at the top of the eastern watershed and lives in the headwaters of the eastwards-flowing Fitzroy River. Whereas the Carnarvon Gorge is situated well south of the known distribution of north-eastern species of *Jardinella*, and the species found there today are morphologically very dissimilar, the existence of *Jardinella* species in non-artesian springs in the Great Dividing Range in the eastern headwaters appears to lend support to the hypothesis that *Jardinella* crossed the Great Divide further north and invaded the coastal rivers.

If the scenario presented above is accepted, the presence of hydrobiids as part of the freshwater fauna in north-east Queensland is a rather recent phenomenon. This observation is supported by the relatively small amount of divergence between the recognised eastern taxa compared with that seen in the western fauna (Ponder & Clark, 1990). Were hydrobiids always absent from the coastal rivers? The presumably

continuous wet habitat in at least parts of this area should have provided refuges for at least some relictual species. So far none have been found. The group has a northern distribution. Hydrobiids are found in the Atea Plateau in the Papua New Guinea highlands (Smith, 1980) and, apart from the present day north-western Queensland spring-associated fauna, Miocene hydrobiid fossils are known from western Queensland and the Northern Territory (McMichael, 1968; Ponder & Clark, 1990).

There has been insufficient collecting in north-east Queensland to make definitive statements about the distribution of the group. However, as prediction should be the test of any robust hypothesis, I predict that additional species of *Jardinella* will be found in permanent springs and streams in the northern parts of the Great Dividing Range providing further links between the eastern and western members of the genus. In addition I predict that if additional freshwater hydrobiid taxa are found in north-eastern Queensland then they will either be derived members of the *Jardinella* radiation or relictual species that are not part of this radiation but more closely related to taxa in south-eastern Australia or New Guinea.

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## APPENDIX

TABLE OF MEASUREMENTS. Measurement data for shells and opercula of *Jardinella* species. The means and standard deviations (S.D.) are given for sexed populations, the number of individuals measured in parentheses. AA – aperture angle; AL – length of aperture; AW – width of aperture; BL – length of body whorl; CV – convexity ratio; OC – length of white smear on operculum; OL – length of operculum; ON – distance of opercular nucleus from the edge opposite the growing edge; PD – protoconch diameter; PW – protoconch whorls; SA – spire angle; SL – shell length; SW – shell width; TW – number of teleoconch whorls; WU – width of umbilicus.

| | SL | SW | AL | AW | BW | WU | CV | SA | AA | PD | PW | TW | OL | ON | OC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *J. thaanumi* | | | | | | | | | | | | | | | |
| Lectotype | | | | | | | | | | | | | | | |
| | 3.25 | 3.03 | 2.00 | 1.98 | 2.92 | 0.16 | 0.22 | 78.71 | 36.25 | 0.39 | 1.25 | 3.00 | – | – | – |
| Adult paralectotypes | | | | | | | | | | | | | | | |
| | 3.40 | 3.05 | 2.14 | 2.09 | 3.01 | 0.21 | 0.23 | 81.30 | 30.60 | 0.39 | 1.25 | 3.00 | – | – | – |
| | 2.84 | 2.69 | 1.78 | 1.61 | 2.62 | 0.24 | 0.29 | 80.12 | 35.25 | 0.43 | 1.25 | 2.90 | – | – | – |
| Figured subadult | | | | | | | | | | | | | | | |
| | 3.06 | 2.77 | 1.95 | 1.76 | 2.73 | 0.15 | 0.22 | 84.20 | 28.60 | 0.44 | 1.25 | 2.60 | – | – | – |
| Barron River Gorge (males) | | | | | | | | | | | | | | | |
| MEAN (6) | 3.27 | 2.98 | 2.09 | 1.90 | 2.95 | 0.26 | 0.23 | 79.25 | 35.85 | 0.38 | 1.23 | 2.90 | 1.64 | 0.46 | 0.56 |
| S.D. | 0.31 | 0.18 | 0.11 | 0.15 | 0.26 | 0.05 | 0.02 | 2.37 | 2.46 | 0.03 | 0.02 | 0.09 | 0.15 | 0.04 | 0.05 |
| (females) | | | | | | | | | | | | | | | |
| MEAN (4) | 3.38 | 3.15 | 2.15 | 1.96 | 3.05 | 0.28 | 0.22 | 79.06 | 34.96 | 0.39 | 1.25 | 2.94 | 1.67 | 0.50 | 0.67 |
| S.D. | 0.21 | 0.21 | 0.18 | 0.19 | 0.18 | 0.03 | 0.02 | 1.38 | 2.70 | 0.02 | 0.00 | 0.08 | 0.06 | 0.04 | 0.09 |
| Douglas Creek (Stn 25) (males) | | | | | | | | | | | | | | | |
| MEAN (2) | 3.89 | 3.64 | 2.55 | 2.24 | 3.51 | 0.35 | 0.23 | 82.84 | 32.96 | 0.42 | 1.25 | 2.88 | 1.85 | 0.52 | 0.36 |
| S.D. | 0.03 | 0.05 | 0.01 | 0.01 | 0.01 | 0.06 | 0.02 | 0.21 | 0.48 | 0.05 | 0.00 | 0.08 | 0.02 | 0.01 | 0.07 |
| (females) | | | | | | | | | | | | | | | |
| MEAN (8) | 3.85 | 3.61 | 2.46 | 2.32 | 3.47 | 0.36 | 0.23 | 81.20 | 34.40 | 0.41 | 1.26 | 2.97 | 1.84 | 0.53 | 0.33 |
| S.D. | 0.12 | 0.09 | 0.10 | 0.09 | 0.10 | 0.06 | 0.01 | 4.14 | 3.34 | 0.02 | 0.04 | 0.07 | 0.07 | 0.04 | 0.04 |
| Dowah Creek (Stn 42) (males) | | | | | | | | | | | | | | | |
| MEAN (4) | 2.78 | 2.56 | 1.70 | 1.58 | 2.47 | 0.18 | 0.25 | 80.97 | 30.40 | 0.39 | 1.25 | 2.71 | 1.35 | 0.40 | 0.38 |
| S.D. | 0.35 | 0.29 | 0.22 | 0.23 | 0.33 | 0.06 | 0.03 | 0.81 | 2.27 | 0.03 | 0.00 | 0.06 | 0.21 | 0.06 | 0.28 |
| (females) | | | | | | | | | | | | | | | |
| MEAN (6) | 2.70 | 2.50 | 1.65 | 1.51 | 2.41 | 0.21 | 0.23 | 83.21 | 30.89 | 0.40 | 1.25 | 2.64 | 1.33 | 0.39 | 0.24 |
| S.D. | 0.32 | 0.21 | 0.20 | 0.16 | 0.25 | 0.08 | 0.01 | 4.30 | 2.88 | 0.01 | 0.00 | 0.20 | 0.10 | 0.03 | 0.14 |
| *J. tumorosa* | | | | | | | | | | | | | | | |
| Types | | | | | | | | | | | | | | | |
| Holotype (female) | | | | | | | | | | | | | | | |
| | 3.30 | 2.94 | 1.86 | 1.75 | 2.78 | 0.29 | 0.27 | 76.70 | 29.10 | 0.41 | 1.25 | 3.10 | 1.65 | 0.54 | 0.50 |
| Figured paratype (female) | | | | | | | | | | | | | | | |
| | 2.83 | 2.78 | 1.67 | 1.72 | 2.47 | 0.21 | 0.23 | 80.50 | 26.90 | 0.37 | 1.25 | 3.00 | 1.57 | 0.46 | 0.38 |
| Figured paratype (female) | | | | | | | | | | | | | | | |
| | 3.74 | 3.23 | 2.24 | 2.17 | 3.23 | 0.27 | 0.22 | 82.40 | 24.10 | 0.40 | 1.25 | 3.10 | 1.78 | 0.53 | 0.74 |
| Summary data (males) | | | | | | | | | | | | | | | |
| MEAN (2) | 3.22 | 2.90 | 2.03 | 1.79 | 2.79 | 0.25 | 0.22 | 77.07 | 24.72 | 0.39 | 1.30 | 2.98 | 1.64 | 0.53 | 0.46 |
| S.D. | 0.22 | 0.12 | 0.09 | 0.08 | 0.16 | 0.03 | 0.03 | 0.97 | 0.11 | 0.04 | 0.05 | 0.03 | 0.03 | 0.03 | 0.10 |
| Summary data (females) | | | | | | | | | | | | | | | |
| MEAN (11) | 3.19 | 2.90 | 1.92 | 1.82 | 2.75 | 0.28 | 0.23 | 77.85 | 26.89 | 0.40 | 1.27 | 2.95 | 1.58 | 0.50 | 0.48 |
| S.D. | 0.26 | 0.18 | 0.15 | 0.14 | 0.21 | 0.05 | 0.02 | 2.43 | 2.53 | 0.04 | 0.04 | 0.13 | 0.15 | 0.05 | 0.11 |
| Pine Creek (Stn 44) (males) | | | | | | | | | | | | | | | |
| MEAN (5) | 3.17 | 2.88 | 1.92 | 1.80 | 2.78 | 0.27 | 0.24 | 82.18 | 27.27 | 0.36 | 1.25 | 2.99 | 1.59 | 0.49 | 0.47 |
| S.D. | 0.12 | 0.14 | 0.10 | 0.06 | 0.10 | 0.07 | 0.02 | 1.93 | 2.71 | 0.01 | 0.00 | 0.10 | 0.09 | 0.02 | 0.07 |
| (females) | | | | | | | | | | | | | | | |
| MEAN (4) | 3.30 | 3.04 | 2.13 | 1.88 | 2.69 | 0.22 | 0.20 | 79.99 | 22.03 | 0.37 | 1.25 | 3.06 | 1.67 | 0.51 | 0.41 |
| S.D. | 0.24 | 0.21 | 0.16 | 0.15 | 0.39 | 0.06 | 0.01 | 2.44 | 4.33 | 0.03 | 0.00 | 0.08 | 0.10 | 0.02 | 0.09 |
| *J. tullyensis* | | | | | | | | | | | | | | | |
| Holotype (female) | | | | | | | | | | | | | | | |
| | 3.51 | 3.09 | 2.10 | 1.92 | 2.96 | 0.33 | 0.26 | 78.00 | 30.50 | 0.40 | 1.25 | 3.00 | 1.76 | 0.55 | 0.59 |

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# The Species of *Pleuroxus* and of Three Related Genera (Anomopoda, Chydoridae) in Southern Australia and New Zealand

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ABSTRACT. Two new chydorid cladoceran genera, *Planicirclus* (n.gen.) with one species *Planicirclus alticarinatus* (n.sp.), and *Plurispina* (n. gen.) with two species, *Plurispina chauliodus* (n.sp.) and *P. multituberculata* (n.sp.), are described from south-western Australia. The status of the chydorid genus *Pleuroxus* in southern Australia and New Zealand is reviewed, with two new species described: *Pleuroxus foveatus* (n.sp.) from south-western Australia, and *P. helvenacus* (n.sp.) from New Zealand. The European species *Pleuroxus aduncus* (Jurine), previously identified from the region, is described, and shown definitely not to occur there. *Pleuroxus hastirostris* Sars and *P. inermis* Sars are redescribed, as is *Archepleuroxus baylyi* Smirnov & Timms. Four other species of *Pleuroxus* described from southern Australia are considered *nomina dubia*. All eight recognised taxa appear to be endemic to the region. Marked differences between the *Pleuroxus* fauna of eastern and western Australia provide evidence for adaptive radiation. It is likely that a comparable high degree of endemicity will be found in other chydorid groups.

FREY, D.G., 1991. The species of *Pleuroxus* and of three related genera (Anomopoda, Chydoridae) in southern Australia and New Zealand. Records of the Australian Museum 43(3): 291–372.

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Cladocerans, small branchiopod crustaceans, are predominantly freshwater in affinity. They are widely distributed in Australasian inland waters, but systematic and ecological studies of them have been few. A major difficulty has been the lack of taxonomic keys to the Australasian fauna, compounded by indiscriminate use of available (northern hemisphere) authoritative references, e.g. Ward & Whipple (revised by Edmondson, 1963) or Pennak (1978). More recently, an appropriate level of resolution of Australian daphniid cladocerans has been achieved by scanning electron microscopy (SEM), e.g. *Simocephalus* (Dumont *in* Smirnov & Timms, 1983) or electrophoretic methods, e.g. *Daphnia carinata* (Benzie, 1986). However, most families of Australasian Cladocera remain poorly resolved.

Identifying species of Chydoridae, in particular, presents problems. If one were concerned with one region, I believed he could define the species easily enough and put unique names on them, but if he were concerned also with equivalence or conspecificity between regions, then the matter becomes much more difficult. Most generic names have had no formal description in the literature, and species names have been transferred from one continent to another. The result is that many species throughout the world are improperly named, and many genera are not monophyletic.

In questioning widely accepted cosmopolitanism in cladocerans (Frey, 1982), I had become convinced that the present distribution of chydorid species in the world was likely influenced in part by the breakup of Gondwana. To investigate this hypothesis I collected intensively in Australia and New Zealand in 1986 to 1987. From more than 400 samples collected, and from almost as many collected previously by other scientists, which I was privileged to examine, I obtained many exceptional populations of various chydorids. The fauna of New Zealand was investigated first, being much less extensive than that of Australia, and *Pleuroxus* was the first genus examined, because only a single species, *P. hastirostris*, had been described from that country.

*Pleuroxus hastirostris* was readily defined, but the New Zealand material contained a second taxon which seemed to resemble *Pleuroxus jugosus* Henry from Australia, as treated by Smirnov & Timms (1983). Deciding the identity of this second taxon thus required a detailed comparison with the Australian taxon, and here is where the problems began. The *Pleuroxus jugosus* of Henry is represented by only a holotype, which is an immature specimen that does not show many of the characters needed for identification. Moreover, Smirnov & Timms (1983) in their expanded description of the taxon mistakenly used a species from a different genus (described in this paper). Additionally, populations from Western Australia differed significantly from the accepted morphology of *Pleuroxus*. It was difficult at first to define the populations by species, much less put names on them.

The final outcome is that two new genera and five new species are described in this paper, with redescriptions of four other taxa described previously. *Pleuroxus aduncus* from Europe is included to provide a contemporary description of the taxon for comparison with the Australian taxa, or with populations from other parts of the world that presently are named *Pleuroxus aduncus*. Although claimed to occur in Australia, it does not (*P. inermis* is closest to it), and neither of the two New Zealand species occurs in Australia. No species named on other continents are present. Thus, here is still another example of non-cosmopolitanism among chydorids where cosmopolitanism previously had been thought to exist. There is a very high rate of endemism, even higher than that indicated by Smirnov & Timms (1983). It seems certain that other new taxa will be discovered, particularly in south-western Western Australia, by collecting in unique kinds of aquatic habitats, including seasonal, weakly to moderately saline, extremely shallow, or those having a variety of other restrictive features.

What these studies indicate is that when examined in detail, the related taxa of a region differ kaleidoscopically in many morphological characters, making it difficult to decide the limits of the species. Australia, because of its very large number of endemic taxa, may be different from the other continents in the amount of such differentiation, but as this is the first such study conducted on any continent, one cannot be certain. It may be that other continents will show a corresponding amount of morphological differentiation among closely related species.

**Fig.1.** Length-frequency distributions by stage of females and instars of males of the populations of the various taxa considered in this study. *Pleuroxus inermis* and *Pleuroxus foveatus* are each represented by several different populations. The other seven taxa are each represented by a single population, although the two taxa from New Zealand – *Pleuroxus hastirostris* and *Pleuroxus helvenacus* – have a few individuals from collections by other persons available for comparison and for including in the descriptions. The early frequency peaks of parthenogenetic females are not labelled specifically, but it should be apparent that they correspond to the prereproductive instars I and II recognised in other chydorids.

Almost 16% of the samples collected in Australia contained one or another species of *Pleuroxus* or related genera, mainly *Pleuroxus inermis*, but only two out of 157 samples collected in New Zealand. Some of the best populations available, which yielded the new species and genera from Western Australia, are from samples collected by I.A.E. Bayly and R.J. Shiel.

## Methods

My personal samples were collected in the littoral region with a pole-mounted net of 120 µm Nitex, the mouth of which was covered with 5 mm mesh bronze screen to keep out large objects. The samples were preserved immediately with commercial formalin (roughly 40% formaldehyde) containing about 4% sucrose by adding 2 to 4 ml to a 125 ml sample, giving a final concentration of about 1% formaldehyde. The collections of Bayly were made with an about 200 µm-mesh dip net and those of Shiel with a 53 µm-mesh Birge cone net. All samples are stored in weak formalin, which seems the best preservative for retaining the exoskeleton and internal organs in good condition. In the laboratory the samples were inventoried at 25x stereo magnification for the various animals they contained. For the anomopods, notes were made on abundance, presence of gamogenetic stages, and any noteworthy details of morphology. The information on the inventory cards enables the best samples for any species to be identified for further study.

For the samples used in this study, aliquots were placed in a petri dish, systematically examined at 25x, and all specimens and exuviae of the *Pleuroxus* species were removed to a depression slide, where they were equilibrated with glycerol. These specimens then were mounted temporarily in glycerol, about 40 per coverslip, for measurement of length and for *camera lucida* drawings of animals and their parts. Fresh exuviae are the best material for revealing the details of the head appendages, trunklimbs, postabdomen and claws, and details of shell sculpturing and setation. The individual parts are dissected away from one another and then mounted either in glycerol or polyvinyl-lactophenol (PVL) stained with lignin pink. Sometimes intact specimens must be dissected for shape of the rostrum and other details of structure, particularly when good exuviae are not available. Specimens from samples collected by other persons were handled in the same manner.

Specimens and their parts were examined on a Wild M20 compound microscope with phase-contrast optics. Measurements were made with an ocular scale calibrated against a micrometer slide (0.1 and 0.01 mm units). Drawings were made with a Wild binocular *camera lucida* calibrated against the same micrometer scale.

For the SEM photographs, specimens were selected, dissected if necessary to reveal the postabdomen, trunklimbs, and head appendages, and then 'washed' with a fine pipette to remove any loose detritus. Most chydorids are clean when alive. If they are rinsed thoroughly in the net to remove particles smaller than about 100 µm, they generally provide excellent material for SEMs. If they are captured with a finer net, or not washed adequately, the fine material gets between the shells and also, over time, becomes firmly fastened to the outside of the animal, where it cannot be removed, at least easily, by detergents. Even weak sonication is too drastic a procedure for chydorids, resulting in the loss of many of the setae.

Documentary specimens, including holotypes and paratypes, placed in museums were mostly mounted in glycerine jelly, with the cover glasses supported by small squares of plastic. Exuviae and dissected parts of specimens were mounted in PVL/lignin pink. All slides were sealed either with Zut or Glyceel to protect the specimens and to curtail loss of water from the PVL mounts.

Specimens of taxa from Australia or New Zealand described by Sars or Henry were borrowed from the Sars Museum in Oslo and the Australian Museum in South Sydney (see Table 1). All tables referred to in this paper are included in the Appendix. The following abbreviations for institutions are used: AM – Australian Museum, Sydney; BM(NH) – British Museum (Natural History), London; NMNZ – National Museum of New Zealand, Wellington; USNMNH – United States National Museum of Natural History, Washington.

## Historical Resumé of Previous Studies

Table 1 lists all the *Pleuroxus* and *Pleuroxus*-like taxa that have been claimed to occur in Australia or New Zealand, including the new taxa from the present study. Four of the first six species claimed to occur in Australia and New Zealand were described from other continents. Of these, *P. denticulatus, P. similis* and *P. laevis* are not considered in this paper because they differ so markedly from all the other species. Besides, since they were described from other continents, a detailed comparison would need to be made between type populations and populations from Australia presently bearing these names. For *P. laevis* this should be relatively easy, as there is now a detailed description of the taxon in the literature (Frey, 1988). Two other taxa were described by Sars (1896, 1903), one species each from Australia and New Zealand. Smith (1909) later described a new species from Tasmania, and Henry (1918, 1922) described five species (three in the genus *Chydorus*) from the Sydney region, all of which tended to be ignored by subsequent workers because of the poor descriptions and illustrations. Her taxon *Chydorus jugosus*, although closely related to the two species here placed in a new genus, cannot be identified from the single immature specimen available. Henry's *Pleuroxus reticulatus* apparently involves two different taxa, neither of which is in the genus *Pleuroxus*. Smirnov & Timms (1983) erected the new genus and species *Archepleuroxus baylyi* but kept everything else in

much the same unresolved state. They synonymised Henry's species with *Pleuroxus aduncus* and *Pleuroxus similis*. The present paper includes *Pleuroxus aduncus* described from Europe but does not include the other three taxa described from other continents. It is suggested, though, on the basis of past detailed studies, that what occurs in Australia will be found to resemble the strict taxa only superficially when adequate comparisons are made.

## Taxonomic Descriptions

### *Pleuroxus* Baird

### *Pleuroxus aduncus* (Jurine)

Figs 2-47

*Monoculus aduncus* Jurine, 1820: 152-153, pl.15, figs 8,9. [See Smirnov (1971) for the numerous subsequent and often confusing entries in the synonymy].

**Remarks.** The conceptual understanding of this species is similar to that of many other chydorids described earlier. Jurine (1820) has a very incomplete description of the taxon, accompanied by two small figures that are reasonably accurate but inadequate for present-day needs. Moreover, none of the specimens Jurine used are still extant. He only collected the taxon from Châtelaine, France.

Since that time, many workers have found populations resembling *P. aduncus* on all continents except Antarctica and have either given them the same name or have described them as new species or varieties. Smirnov (1971) aggregated seven species and four varieties with *P. aduncus*, recognising four subspecies, some of which (such as *P. aduncus laticaudatus*) do not seem to belong to the same species. Later (*in* Smirnov & Timms, 1983) he synonymised three more species with *P. aduncus*. In this latter paper he stated that *P. aduncus* "...is a polymorphic species or a complex of related forms...", based in part on an analysis by Harding (1955). Hence, to define the taxa that occur in Australia, which include *P. aduncus* and *P. inermis*, the latter having been synonymised with *P. aduncus* (Smirnov, 1971) but later (Smirnov & Timms, 1983) re-established as a separate species, it is necessary first to define the European taxon more closely to facilitate comparisons.

**Material examined.** The species was described from France, but all our collections are from northern Europe. However, as only one *aduncus*-like species is claimed to occur in Western Europe, the population from Denmark used here can be considered typical for the taxon. The sample selected out of the many available is 3004 from Langemose, which is located between 4 and 5 km on the road from Helsingør to Helsinge, Sjælland, Denmark, collected 23 October 1971. It yielded about 70 specimens, including ephippial females and instars II and III of males.

**Disposition of specimens.** One slide each of a parthenogenetic female, an ephippial female, an instar-II male, and a mature male, mounted separately in glycerine jelly, have been deposited in the following museums. The numbers given are the catalogue or registration numbers of the specimens.

| | AM | NMNZ | BM(NH) | USNMNH |
|---|---|---|---|---|
| parthenogenetic female | P39453 | Cr. 6412. | 1989.600 | 242113 |
| ephippial female | P39454 | Cr. 6413 | 1989.601 | – |
| instar-II male | P39455 | Cr. 6414 | – | – |
| mature male | P39456 | Cr. 6415 | 1989.602 | 242113 |

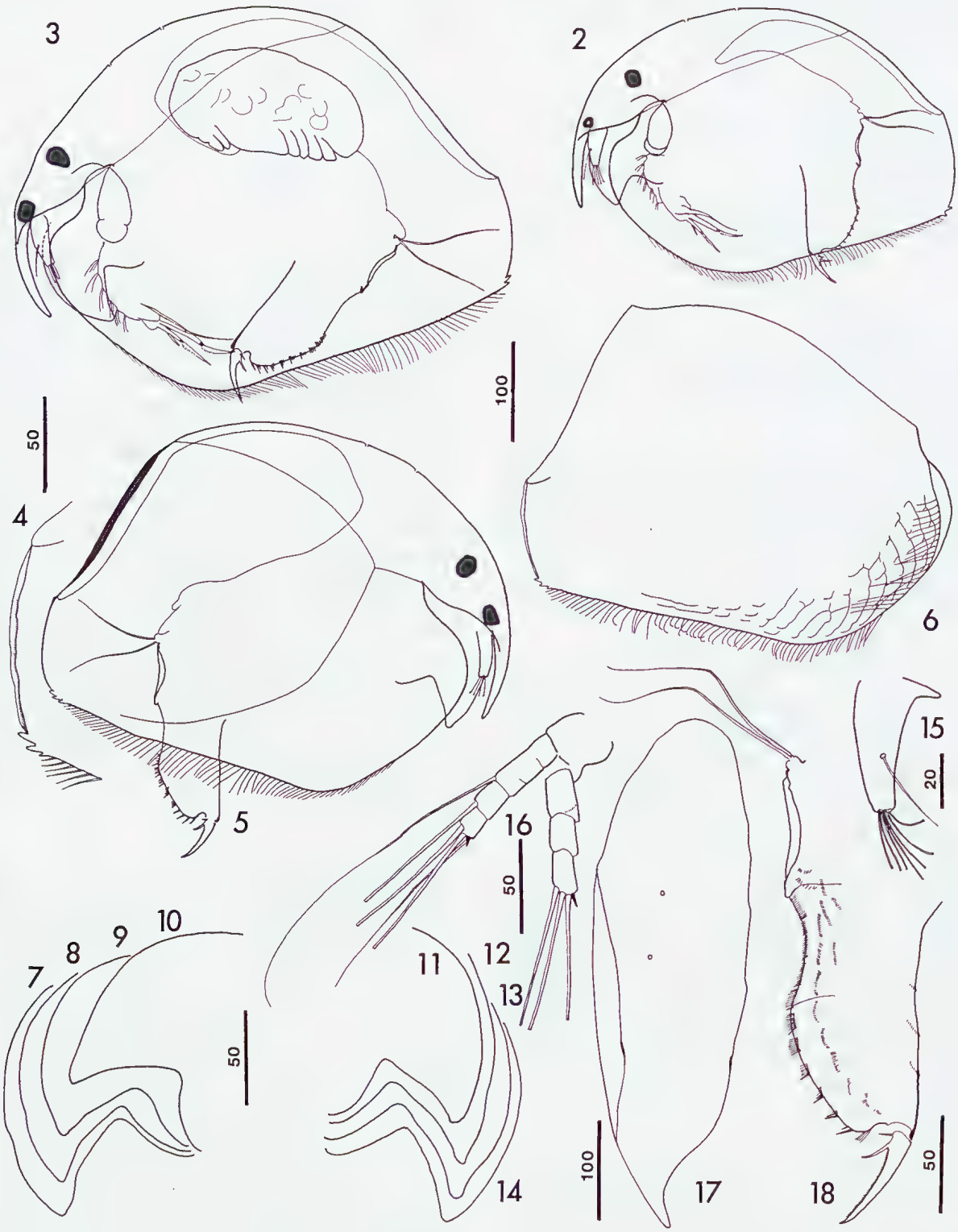
**Diagnosis.** Longer than high. Dorsal margin broadly arched, slightly concave near posterior-dorsal angle; 0-4 teeth (most commonly 2) at posterior-ventral angle; posterior margin short, distinctly convex; ventral margin with pronounced ventral bulge in anterior half; about 10 curved striae in anterior-ventral portion of shell. Rostrum elongate, bluntly tipped. Labral plate large; tip attenuated, narrowly rounded. Postabdomen with 7-10 denticles along postanal margin, each usually accompanied by 1 or more setae, forming clusters that distally are oriented obliquely, proximally are parallel to margin. Abdominal setae long, reaching about halfway in anal groove. Eight setae on antennae; one of terminal setae on endopodite much shorter than others, seta from basal segment very long; terminal spines very short, indistinct. Rounded process extending backward from base of antennule. Males II and III more elongate than females; maximum height at or slightly in front of ventral bulge; postabdomen of mature male tapered distally to base of claws, provided with diagonal groups of setae at margin, a few distal setae thickened into respectable denticles; genital pore terminal near base of claws; seemingly only 1 basal spine on claw.

**Parthenogenetic female.** *Shape and shell* (Figs 2-6, 33, 38, 39). Maximum dorsal curvature posterior to ventral bulge; slight concavity just before posterior-dorsal angle; posterior margin short, weakly and evenly convex, only about one third total height of animal; 0-3 denticles on shell [0,2 (2); 1,1 (3); 1,2 (10); 1,3 (4); 2,2 (13); 2,3 (3); 3,3 (1); 1 immature female with 4 on one side], when multiple tending to occur more on posterior margin than at posterior-ventral angle; distinct line closely paralleling posterior margin, provided with fine spinules beginning immediately after denticles, continuing well toward posterior-dorsal angle (Figs 4, 33, 38, 39); ventral margin with 84 (range 79-89, n=19) marginal setae, including about 10 directed inward along anterior margin (Fig.6); anterior-ventral quarter of shell with about 10 irregularly curved striae; generally a slight bulge in lateral outline each over eye and ocellus.

*Head.* Headshield elongate, narrowed and rounded posteriorly (Fig.17); postpore distance (from posterior headpore to margin of headshield, hereafter PP) about 3 times interpore (IP) distance (n=5); minor pores about

one pore diameter apart; rostrum tapered to bluntly rounded tip (Fig.35); eye somewhat larger than ocellus, which is closer to eye than to tip of rostrum; no markings on head.

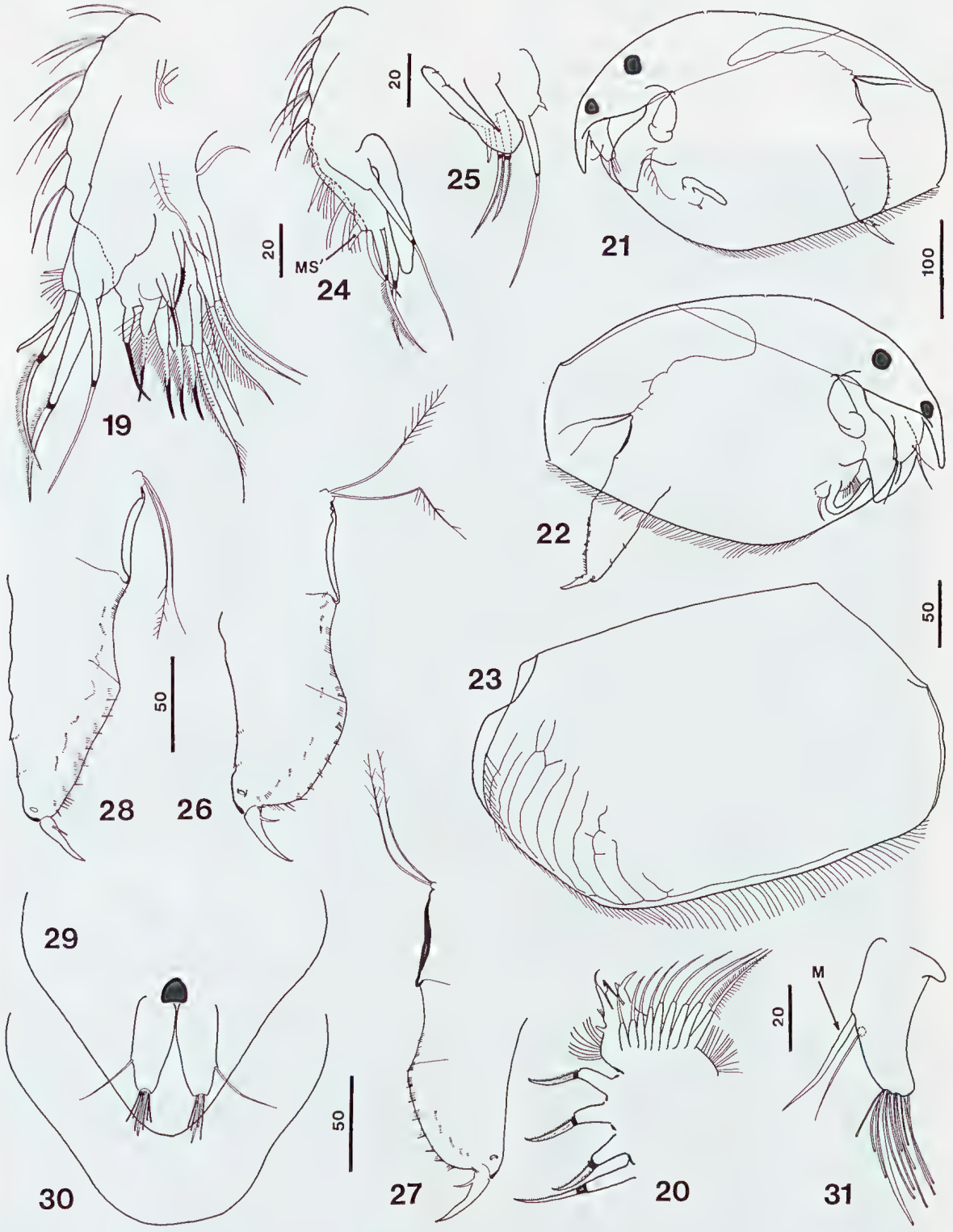
*Antennule* (Figs 2-4, 15, 35). Elongate, slightly curved, tapering distally; base provided with round-tipped projection extending backward (Fig.15); 9 aesthetascs, one thicker and longer than others; antennular seta arises about one third to two fifths from tip, longer than any aesthetasc; all aesthetascs terminate well before tip of




**Figs 2-18.** *Pleuroxus aduncus* (Jurine, 1820). All specimens are females from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 2. instar-II female; 3. mature parthenogenetic female; 4. posterior margin of shell and posterior-ventral angle of mature parthenogenetic female; 5. ephippial female; 6. shell of parthenogenetic female; 7-14. labra of parthenogenetic females; 15. antennule; 16. antenna; 17. headshield; 18. postabdomen and postabdominal claw.

rostrum.

*Antenna* (Figs 16, 35). Formula: 0-0-3(1)/1-1-3(1). Expopodite with 3 almost equally long terminal setae; endopodite also with 3 terminal setae, one much shorter than other 2; middle segment with a seta as long as distal setae; basal segment with a more slender but still long



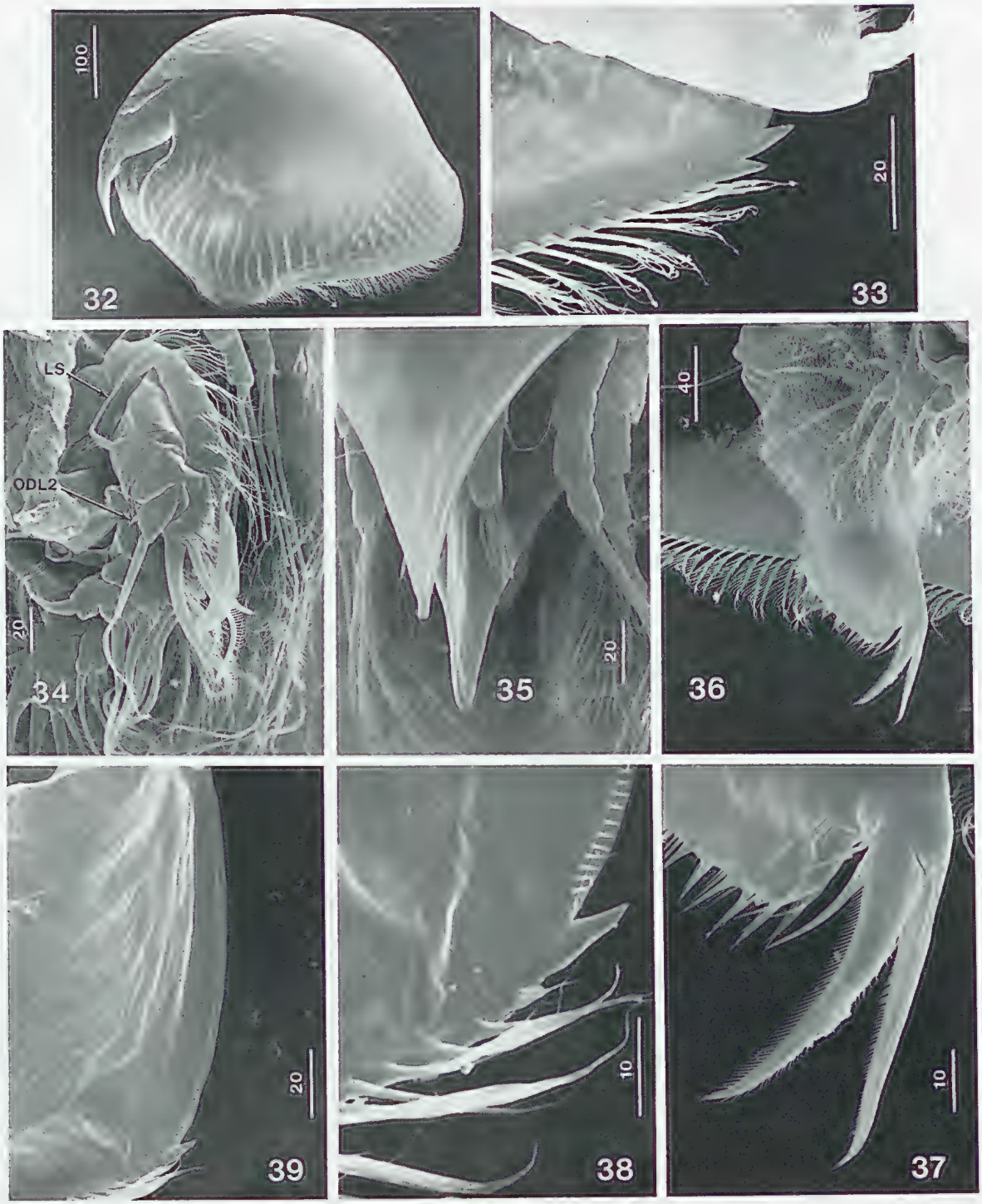

**Figs 19-31.** *Pleuroxus aduncus* (Jurine, 1820). All specimens are from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 19. trunklimb I of parthenogenetic female (ODL2 not visible); 20. part of trunklimb II of parthenogenetic female; 21. instar-I male; 22. mature male; 23. shell of mature male; 24. part of trunklimb I of instar-II male (MS', anlage of male seta on IDL); 25. part of trunklimb I of mature male; 26, 27. postabdomen of instar-II male; 28. postabdomen of mature male, showing the attenuation toward the claws, and the marginal setae arranged mostly in rows oriented diagonally to margin; 29. rostrum and antennules of instar-II male; 30. rostrum of mature male; 31. antennule of mature male, showing the long, unfeathered male seta (M) and the 12 unequal aesthetascs.

and functional seta; small, inconspicuous terminal spine on each branch, exopodite spine slightly larger; spine from basal segment very small, obscure.

*Labrum* (Figs 7-14). Keel broadly expanded, convex anteriorly, sometimes slightly concave near tip, which is narrowed and rounded; posterior margin concave; posterior angle rather narrow, generally about 90°.

*Trunklimb I* (Figs 19, 34, 44). Two outer distal lobe (ODL) setae, one very short and often not visible; 3 inner distal lobe (IDL) setae, 2 long, provided with row of short setules along distal segment, shortest barely as long as basal segments of other two. Middle seta of middle group of corm setae much the longest; all 3 accessory setae well developed; lateral seta very thin and fragile, as long as IDL setae (Figs 19, 34).

*Trunklimb II* (Fig.20). Usually 8 setae in gnathobasic

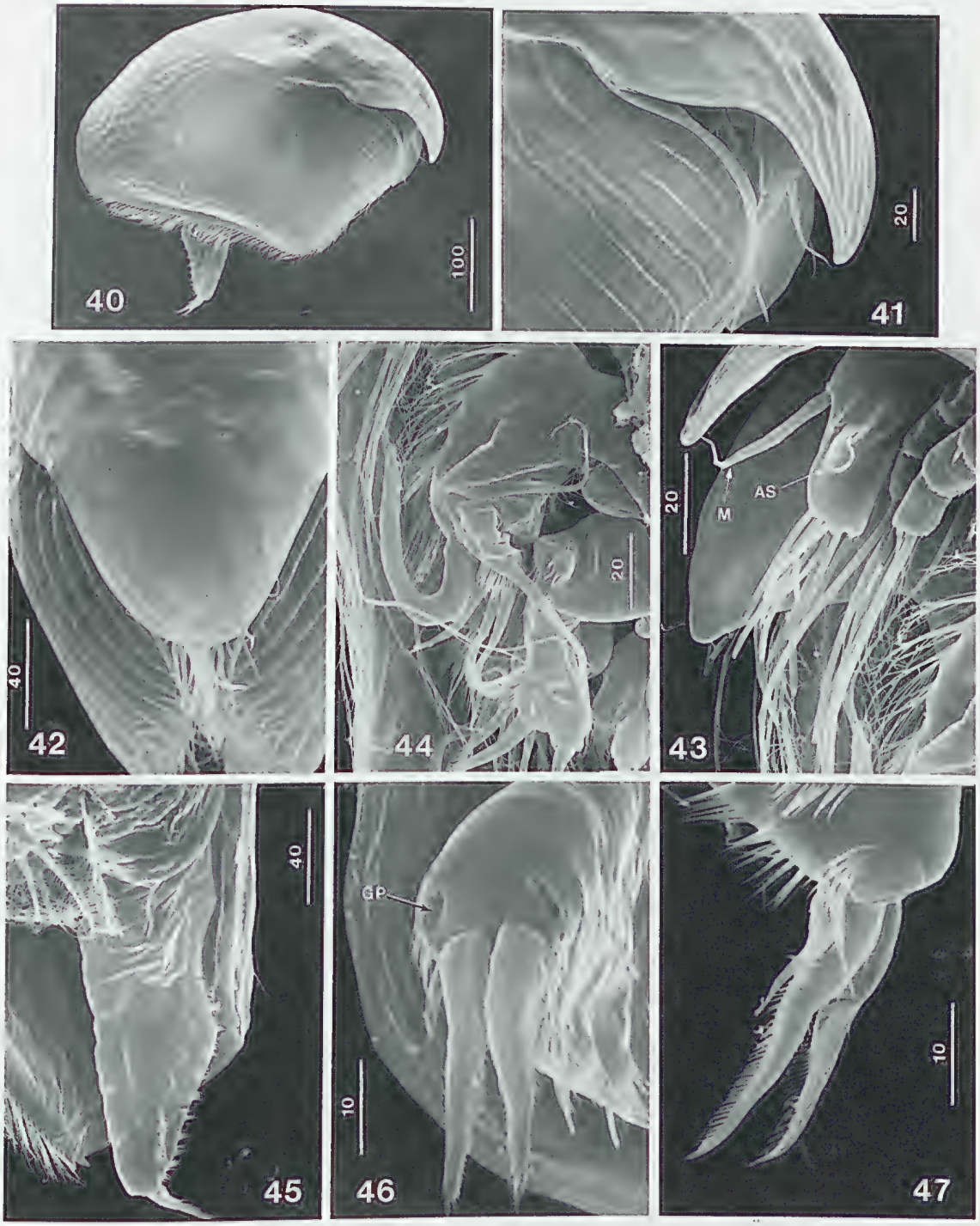



**Figs 32-39.** *Pleuroxus aduncus* (Jurine, 1820). All specimens are from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 32. ephippial female; 33. posterior-ventral angle of mature male; 34. trunklimb I of ephippial female (LS, lateral seta; ODL2, short, unfeathered seta on ODL); 35. tip of rostrum, labrum, and head appendages of ephippial female; 36, 37. postabdomen and claws of parthenogenetic female; 38, 39. posterior-ventral angle with tooth and inner side of posterior margin of shell of ephippial female.

filter comb (specimen drawn has 9); first 3 scraping spines subequal in length, much shorter than spine 4, all provided with small, virtually uncountable marginal setules along distal segment.

*Trunklimbs III-V.* Eight, 6 and 4 gnathobasic filter setae, respectively; 7, 7 and 4 feathered exopodite setae, respectively. Other morphology quite indistinguishable from that of other *Pleuroxus* species.

*Postabdomen* (Figs 18, 36, 37). Preanal and anal portions subequal in length, both shorter than postanal portion; preanal portion with transverse expansion beginning shortly anterior to preanal angle; anal groove concave; postanal angle rounded; dorsal postanal margin weakly convex, tapering distally to rounded distal angle; ventral margin with 2 (possibly 3) transverse crescents of spinules. About 7-10 groups of marginal setae,




**Figs 40-47.** *Pleuroxus aduncus* (Jurine, 1820). All specimens are mature males from Frey sample 3004 (Langemose, Denmark, 23 Oct. 1971). 40. side view; 41. head end, showing rostrum, labrum, and antennule; 42. rounded rostrum; 43. head end of dissected specimen, showing rostrum, antenna, and antennule, the latter with a long, unfeathered male seta (M), antennular seta (AS), and unequal aesthetascs; 44. trunklimb I (MS, male seta; LS, lateral seta); 45. postabdomen; 46. distal end of postabdomen and claws (GP, genital pore); 47. postabdominal claws, showing sigmoid shape and irregular shape of longer basal spine.

distalmost member of each group thickened, denticle-like; several unthickened setae distal to last denticle around tip of postabdomen; anal groove bordered by about 5 successive rows of setules; single row of crescents of spinules along postanal and distal half of anal margins; a few more crescents near preanal angle. Abdominal setae long, reaching to about mid-anal groove, or slightly beyond, when extended.

*Postabdominal claw* (Figs 18, 37). Long, relatively straight; dorsal and ventral margins weakly and regularly curved; dorsal margin with row of fine spinules; 2 basal spines, longer one curved outward, longer than basal width of claw (Fig.37); shorter one straight, very slender, about half as long.

**Ephippial female** (Figs 5, 32). Laterally more compressed than parthenogenetic female; dorsal margin thickened in typical fashion; marked change in curvature between shell and headshield; headshield more elongate and narrowed, with sharp triangular expansion at top of slough line; ephippium with only light pigmentation; no detectable patterning or sculpturing of shell of ephippium; shell flaps narrowly attached to ephippium posteriorly, easily lost.

**Male** (Figs 21, 22, 40). In instar-II, rostrum shortened (compared with female) and broadly rounded at tip (Fig.29); postabdomen similar to female except for irregular ventral margin and bulge near tip ventrally to accommodate genital pore (Figs 26, 27); trunklimb I with typical setae and 2 anlagen of setae (Fig.24) that become functional in instar-III (Figs 25, 44); short anlage of male setae on antennule. In instar-III (= mature), rostrum still shorter, tip broader, truncately rounded (Figs 30, 42); antennule with a long seta, located slightly proximal from antennular seta (Figs 31, 41, 43); 12 aesthetascs (although another antennule seemed to show only 9), one of which is longer and stouter than others; copulatory hook with 3 curved crescents at inner tip (Fig.44); postabdomen more slender than in female, tapered postanally to base of claw, provided with about 7 oblique rows of spinules (Figs 28, 40, 45); genital pore terminal near ventral margin (Figs 46, 47); claw shorter and somewhat stouter than in female, somewhat sigmoid in outline, and seems to have just a single basal spine (Figs 28, 46, 47); ventral margin irregular.

**Length.** Females: overall 0.34-0.60 mm (n=72); instar-I 0.34-0.37 mm (n=11); instar-II 0.42-0.46 mm (n=10); mature 0.48-0.60 mm (n=35); smallest with eggs 0.48 mm; ephippial 0.52-0.60 mm (n=4). Males: instar-II 0.39-0.42 mm (n=4); mature 0.42-0.46 mm (n=8).

**Comments.** Thus, *P. aduncus sensu stricto* is considerably less high than long, with both posterior-dorsal and posterior-ventral angles well developed, the former accentuated by a slight concavity nearby in the dorsal margin and the latter by none to four conspicuous teeth, which occur at the angle, or, if multiple, low along the posterior margin. The ventral margin is not straight but has a marked bulge or expansion anterior to the middle. The shell is smooth except for the ten or so curved striae near the anterior end. The postabdomen has thin denticles, which are always multiple. The labrum is quite broad and the tip not strongly attenuated. The preanal margin of the postabdomen has only a very short section near the anus that is not expanded laterally. The postabdomen of the male is strongly tapered postanally and is provided with seven or eight mostly oblique rows of setae. The postpore distance of mature females is only about three times the interpore distance. There is no keel on the head or shell.

*Pleuroxus aduncus sensu stricto* has a pattern of morphology not seen in any population from Australia. The claim that *P. aduncus* occurs in this part of the world must be based on an inadequate comparison of the populations from Australia and Europe, using only a few general characters readily visible, and guided by the mistaken belief that chydorids are distributed readily by their resting eggs so that the same species can occur easily on different continents.

### *Pleuroxus inermis* Sars

Figs 48-147

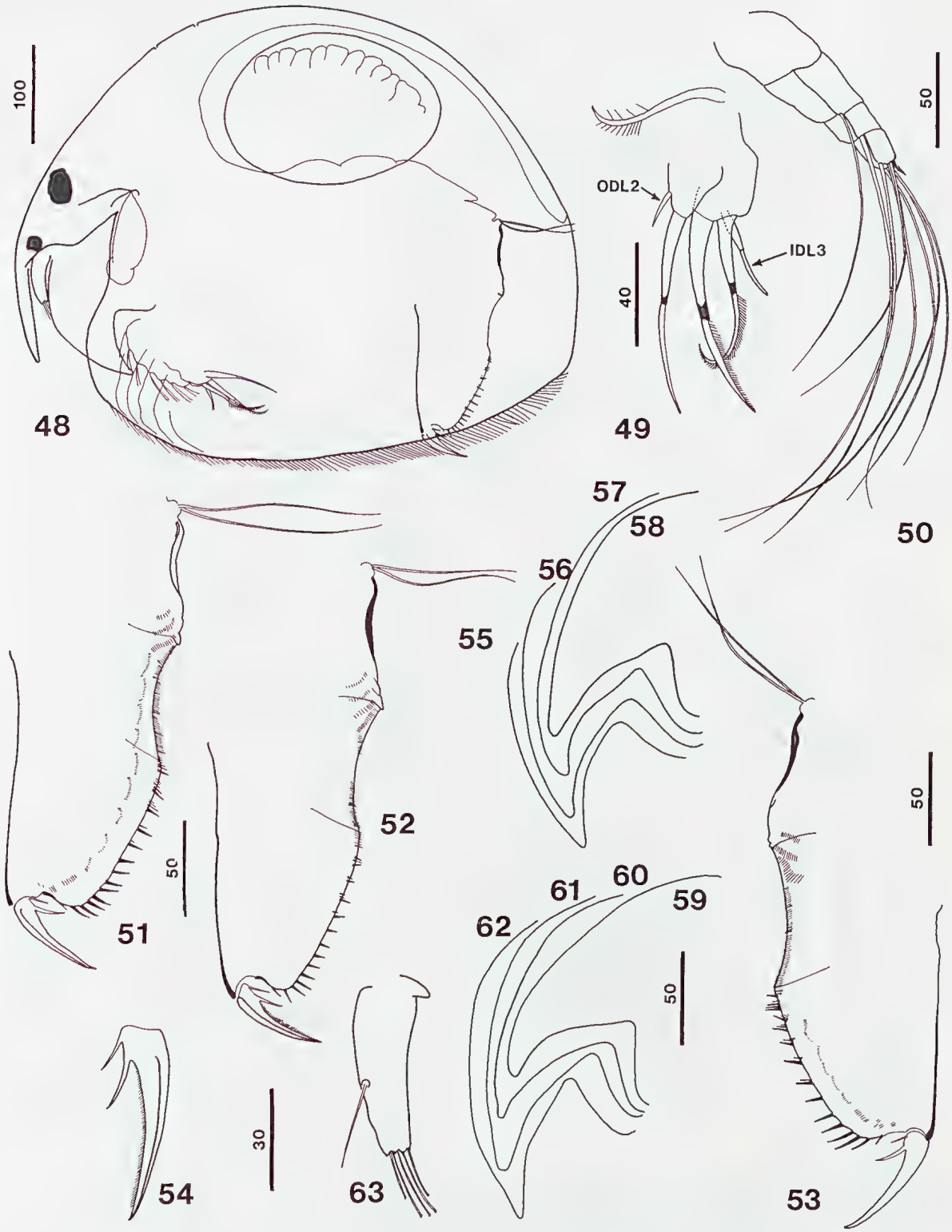
*Pleuroxus inermis* Sars, 1896: 31-35, pl.5, figs 8-9.–Haase, 1903: 150, fig.6.–Sars, 1916 (Africa): 342-343, pl.41, figs 2, 2a-2b.–Henry, 1922: 44-45.–Smirnov & Timms, 1983: 25, fig.24.

*Pleuroxus aduncus*.–Smirnov, 1971: 221 (not *Monoculus aduncus* Jurine, 1820).

**Remarks.** Sars named this species *Pleuroxus inermis* because he thought the taxon lacked a tooth (or teeth) on the shell, the presence of which is characteristic of most other species of *Pleuroxus*. However, a tooth is present on many specimens, even those in the Sars samples. It is generally very small, arising submarginally, and often oriented along the margin of the shell so that frequently it is visible with great difficulty using standard optics, although more readily visible with phase optics. Its presence is variable. Frey sample 7961 from South Australia has almost every individual with a small tooth, whereas Frey sample 8026 from Western Australia has only the occasional individual with a tooth. Such differences may have resulted from at least partial isolation of populations in Western Australia from those in the east.

This seems to be the commonest and most widespread species of *Pleuroxus* in the southern part of Australia. It is relatively small, highly arched but unkeeled, without shell markings except for eight to ten curved striae roughly paralleling the anterior margin of the shell. It has either one minute tooth on the shell or none, and it has the postabdomen tapering and the postanal margin provided with about 12 long, slender denticles, of which the distal ones are all single and the proximal ones multiple. Sars (1889) at first thought this species was the same as King's (1853)

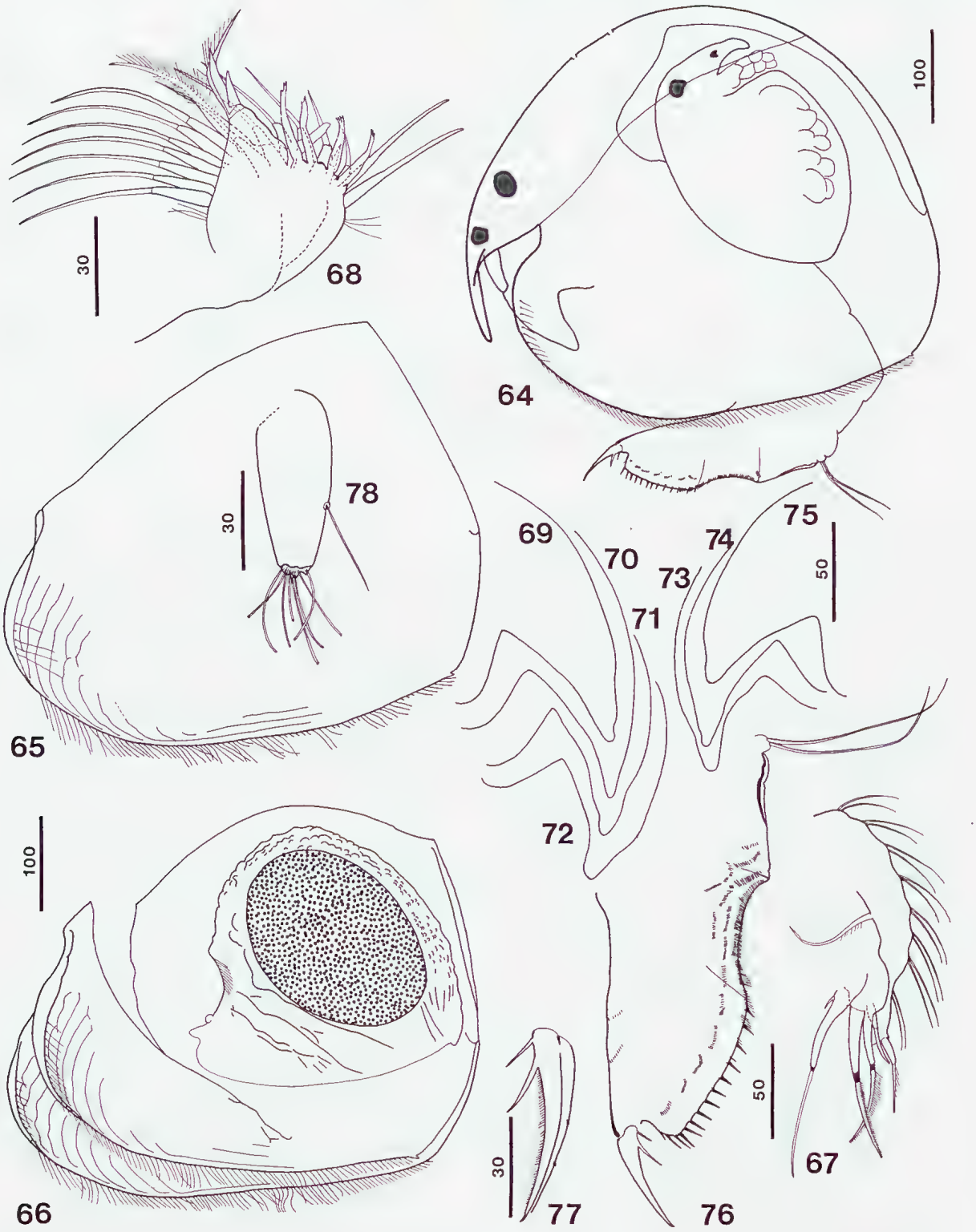
*Chydorus augustus*, but later he decided King's species was *Chydorus globosus* (Sars, 1888). He considered the taxon closely related to *Pleuroxus aduncus* of Europe but separated from it by a number of distinctive characters, which he specified. Smirnov (1971) considered *P. inermis* a synonym of *P. aduncus*, but then later (Smirnov & Timms, 1983) restored it to full species status. It is really quite different from *P. aduncus*, as detailed at the end of this section, and should not be confused with it.



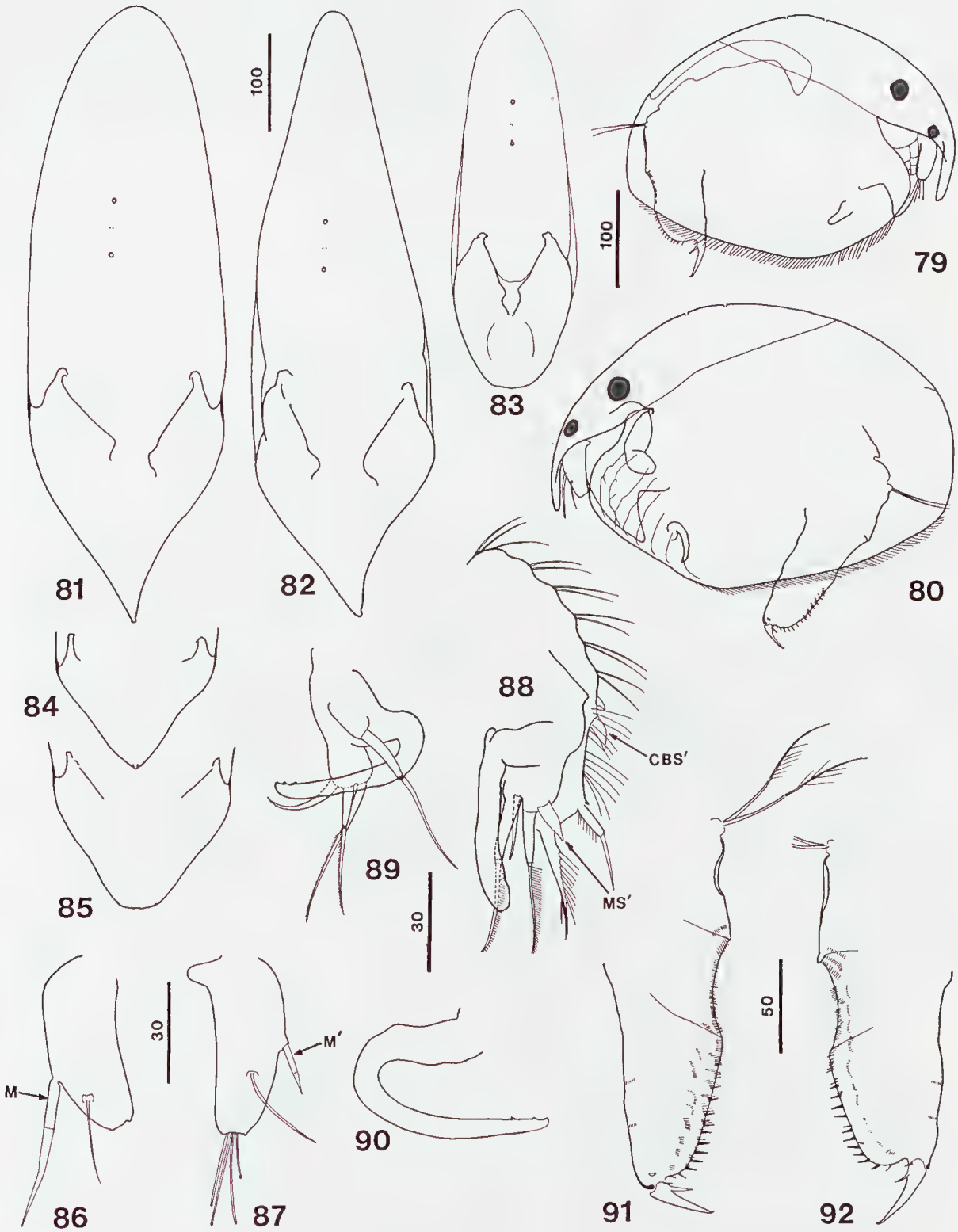

**Figs 48-63**. *Pleuroxus inermis* Sars, 1896. All specimens are parthenogenetic females from Sars sample F4139, raised from dried mud collected by Th. Whitelegge near Waterloo, NSW, about 1892. 48. side view of LECTOTYPE; 49. trunklimb I (ODL2, unfeathered, short ODL seta; IDL3, third seta on IDL, unfeathered); 50. antenna; 51-53. postabdomen (lateral crescents of setules not discernible in Fig.52, which is from LECTOTYPE); 54. postabdominal claw; 55-62. labra; 63. antennule (number of aesthetascs could not be distinguished).

All the records of this taxon are from Australia, except for Sars' 1916 record from South Africa. However, Sars' figure of the taxon in this paper does not match the shape of *P. inermis* from Australia, being less high, and hence may be a different taxon.

**Material examined.** 1. Sars' slides: a. F9671, Victoria, 15 specimens, all of which are in small bits of mounting medium. The specimens are not useable without remounting; b. F9672, Bourke Street, Waterloo, Whitelegge, 5 specimens in balsam, all good. One has been selected as the LECTOTYPE of the taxon; c. F11731,




**Figs 64-78.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 8026 from a natural pond near Waroona, WA, collected 20 Nov. 1986. All figures are of parthenogenetic females except Fig.66. 64. side view; 65. shell of parthenogenetic female; 66. ephippium, showing dimples resulting from contraction of brood pouch lining; 67. trunklimb I; 68. gnathobasic portion of trunklimb III; 69-75. labra; 76. postabdomen; 77. postabdominal claw; 78.antennule.

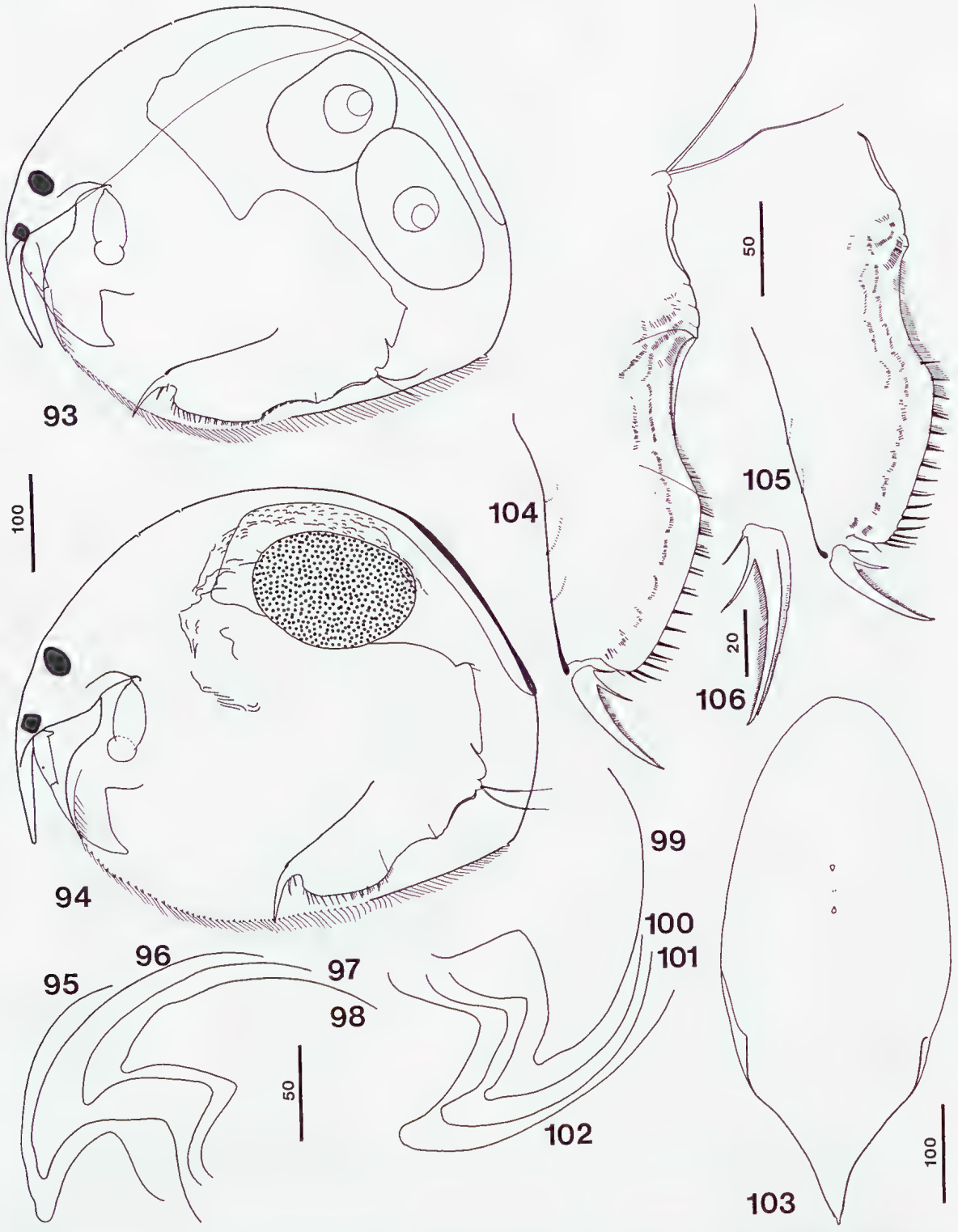



**Figs 79-92.** *Pleuroxus inermis* Sars, 1896. All specimens from Frey sample 8026 (natural pond near Waroona, WA, 20 Nov. 1986). 79. instar-I male; 80. mature male; 81. headshield of parthenogenetic female; 82. headshield of ephippial female; 83. headshield of mature male; 84. rostrum of instar-II male; 85. rostrum of mature male; 86. antennule of mature male, showing a greatly elongate but smooth male seta (M); 87. antennule of instar-II male, showing substantial anlage of male seta (M'); 88. part of trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 89. ODL and IDL of trunklimb I of mature male (MS, male seta; IDL3 not visible, nor was ODL2); 90. copulatory hook of mature male,showing three transverse ridges or crescents near tip; 91. postabdomen of mature male; 92. postabdomen of instar-II male (genital pore not discernible).

Victoria 14, 13 specimens, including several ephippial females; 9 are in clear medium and useable, the other 4 are varyingly obscured by bubbles.

2. Sars' liquid samples: a. F4137, Sydney, Australia, 14 parthenogenetic females; b. F4139, coll. Th. Whitelegge, 201 specimens, nearly all parthenogenetic females carrying eggs; c. F4140, coll. S. Ramsay, 46 parthenogenetic females.

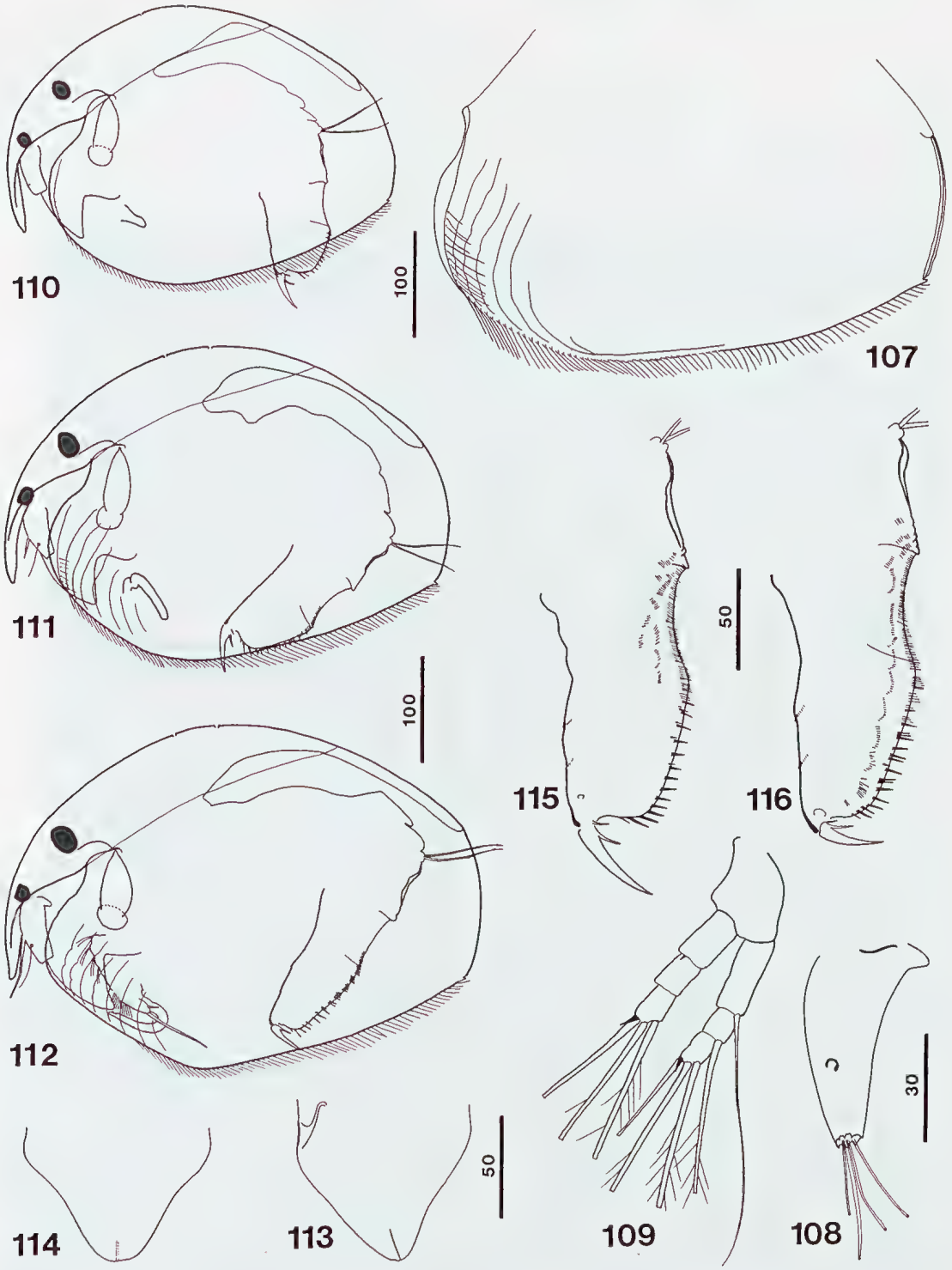
Although a number of these samples have incomplete locality information and dates, slide F9672 and liquid sample F4139 are most significant, because they derive from material (mud?) collected by Th. Whitelegge near Sydney. Liquid sample F4140 was collected by Prof. S. Ramsay, who is the other




**Figs 93-106.** *Pleuroxus inermis* Sars, 1896. All specimens, except Fig.94, are parthenogenetic females from Frey sample 7961 (Wellington ferry crossing, River Murray, SA, 6 Nov. 1986). 93. parthenogenetic female; 94. ephippial female; 95-102. labra; 103 headshield of parthenogenetic female; 104, 105. postabdomens; 106. postabdominal claw.

person mentioned in Sars' description, and sample F4137 is from Sydney, possibly collected either by Ramsay or Whitelegge. Slides F9671 and F11731 from Victoria represent material acquired by Sars subsequent to the 1896 paper and are not mentioned in any of his later papers. It is likely that most of the specimens on slides and in the liquid samples were raised from dried mud.

3. Frey 7961 from the Wellington ferry crossing of the Murray River, SA, collected 6 Nov. 1986. 235



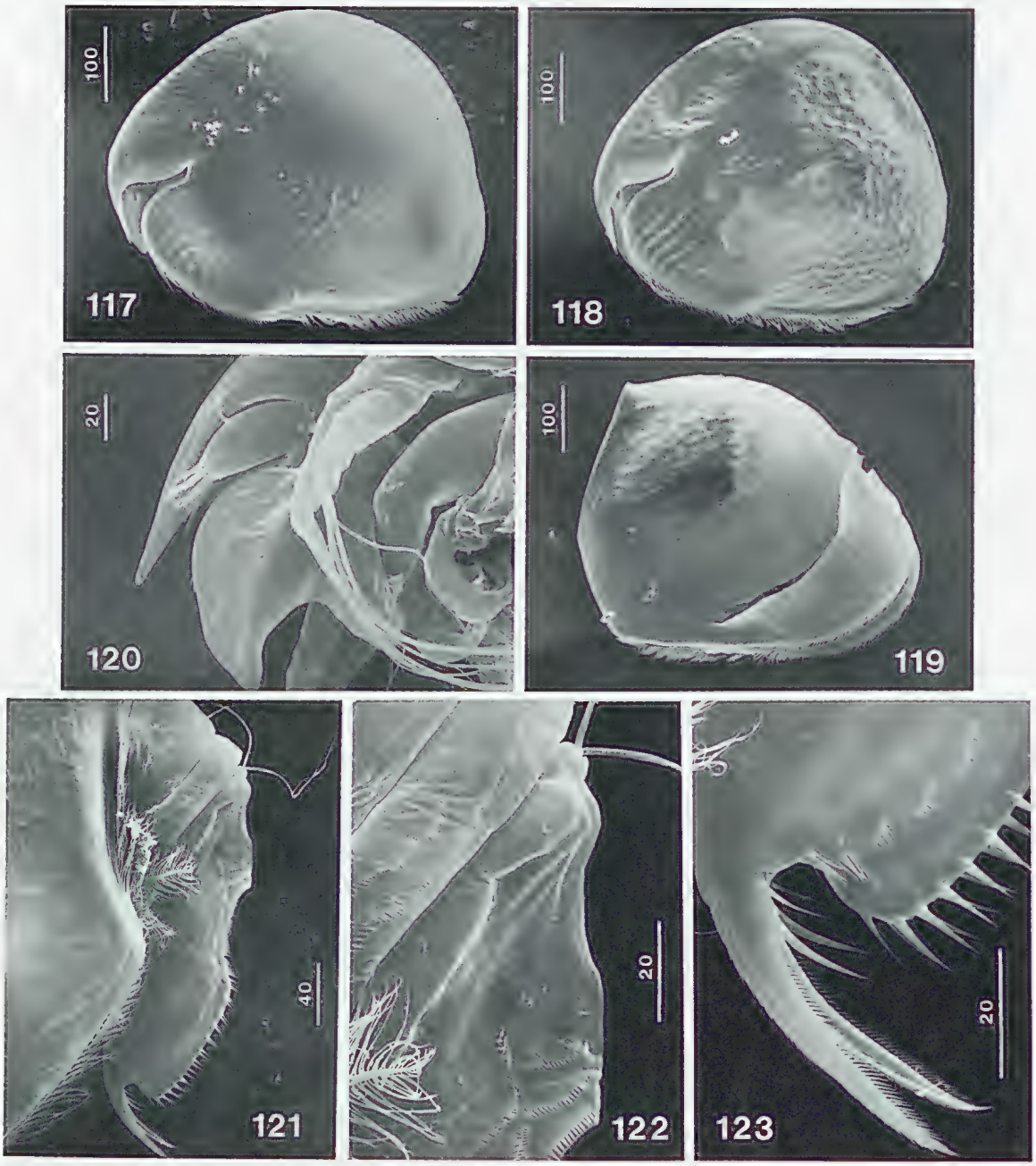

**Figs 107-116.** *Pleuroxus inermis* Sars, 1896. All specimens from Frey sample 7961 (Wellington ferry crossing, River Murray, SA, 6 Nov. 1986). 107. shell of parthenogenetic female; 108 antennule of parthenogenetic female; 109. antenna of parthenogenetic female, showing relatively small size of all three spines and relatively short length of basal endopod seta; 110. instar-I male; 111. instar-II male. 112. mature male; 113. rostrum of instar-II male; 114. rostrum of mature male; 115. postabdomen of instar-II male; 116. postabdomen of mature male (note much shortened postabdominal claw).

specimens, including ephippial females and all 3 instars of males, were removed from the estimated thousands of specimens in the sample.

4. Frey 8026 from a natural pond on Coronation Road from Waroona west to coast highway 1, WA, collected 20 Nov. 1986. This sample yielded a total of 221 specimens, including ephippial females and all three instars of males.

**Types.** LECTOTYPE – the top specimen, which is the middle one of five, on Sars' slide F9672 from Bourke Street, Waterloo, collected by Th. Whitelegge about 1892. A parthenogenetic female 0.59 mm long, well preserved; PARALECTOTYPES – the other four parthenogenetic females on Sars' slide F9672, ranging in length from about 0.57 to 0.62 mm. The length could only be approximated, because the rostrum had been extended forward by coverglass pressure.

**Disposition of other specimens.** Slides of 1 parthenogenetic female from Sars' sample F4139, 1 parthenogenetic female, 1 ephippial female, 1 instar-II male, and 1 mature male from Frey sample 7961, and 1 parthenogenetic female from Frey sample 8026, all mounted separately in glycerine jelly, have been placed in the following museums. The numbers given are the



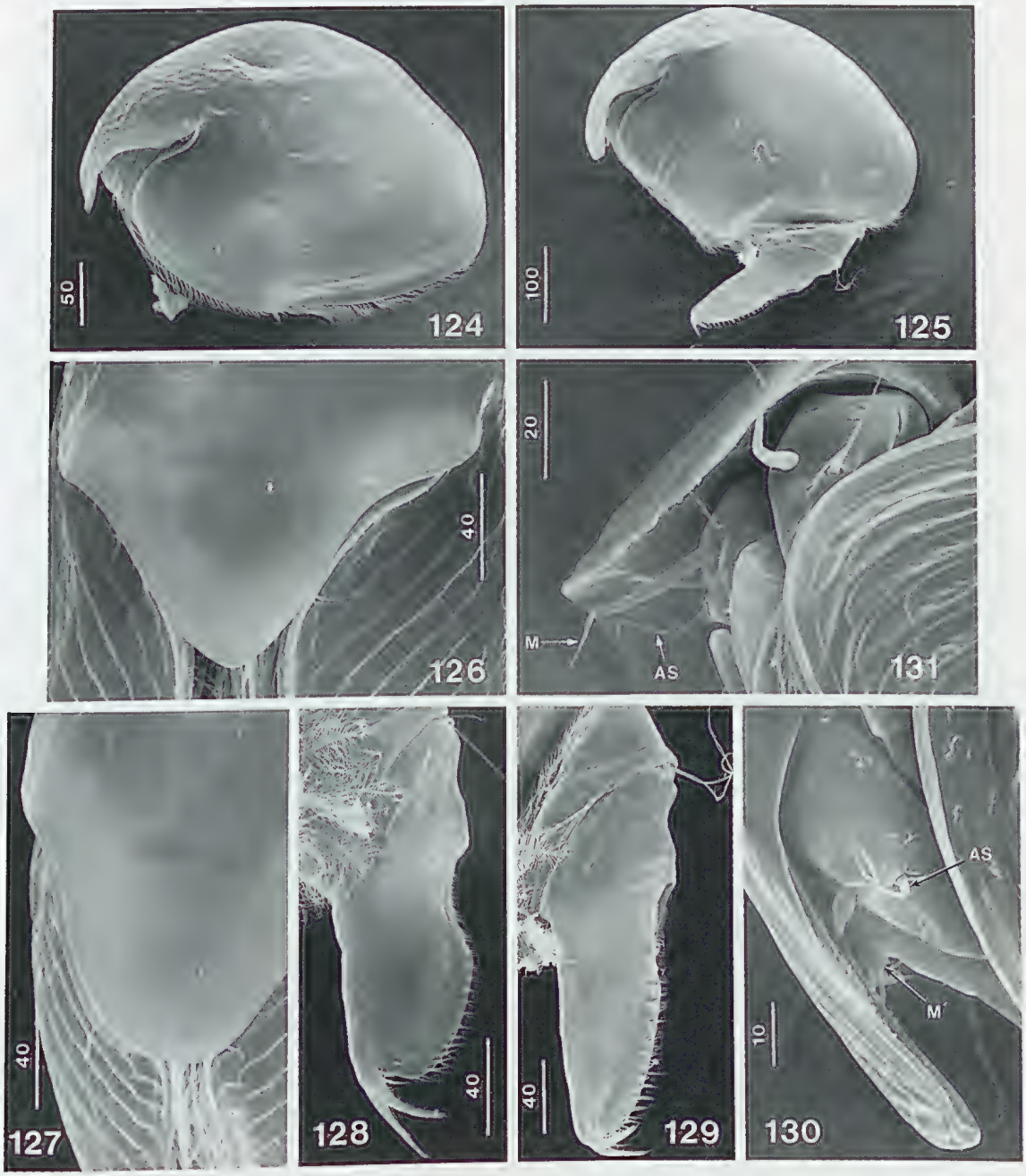

**Figs 117-123.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 8026 (natural pond near Waroona, WA, 20 Nov. 1986). 117. parthenogenetic female; 118. ephippial female; 119. ephippium; 120. head end of dissected parthenogenetic female, showing antennule, antenna, labrum, mandible, and maxilla; 121, 122. postabdomen of parthenogenetic female (note that most denticles, at least distally, are single); 123. postabdominal claw.

catalogue or registration numbers.

| | AM | NMNZ | BM(NH) | USNMNH |
|---|---|---|---|---|
| Sars F4139 | | | | |
| parthenogenetic female | P39457 | Cr. 6416 | 1989.603 | 242114 |
| Frey 7961 | | | | |
| parthenogenetic female | P39458 | Cr. 6417 | 1989.604 | 242115 |
| ephippial female | P39459 | Cr. 6418 | 1989.605 | 242115 |
| instar-II male | P39460 | Cr. 6419 | 1989.606 | 242115 |
| mature male | P39461 | Cr. 6420 | 1989.607 | 242115 |
| Frey 8026 | | | | |
| parthenogenetic female | P39462 | Cr. 6421 | 1989.608 | 242116 |

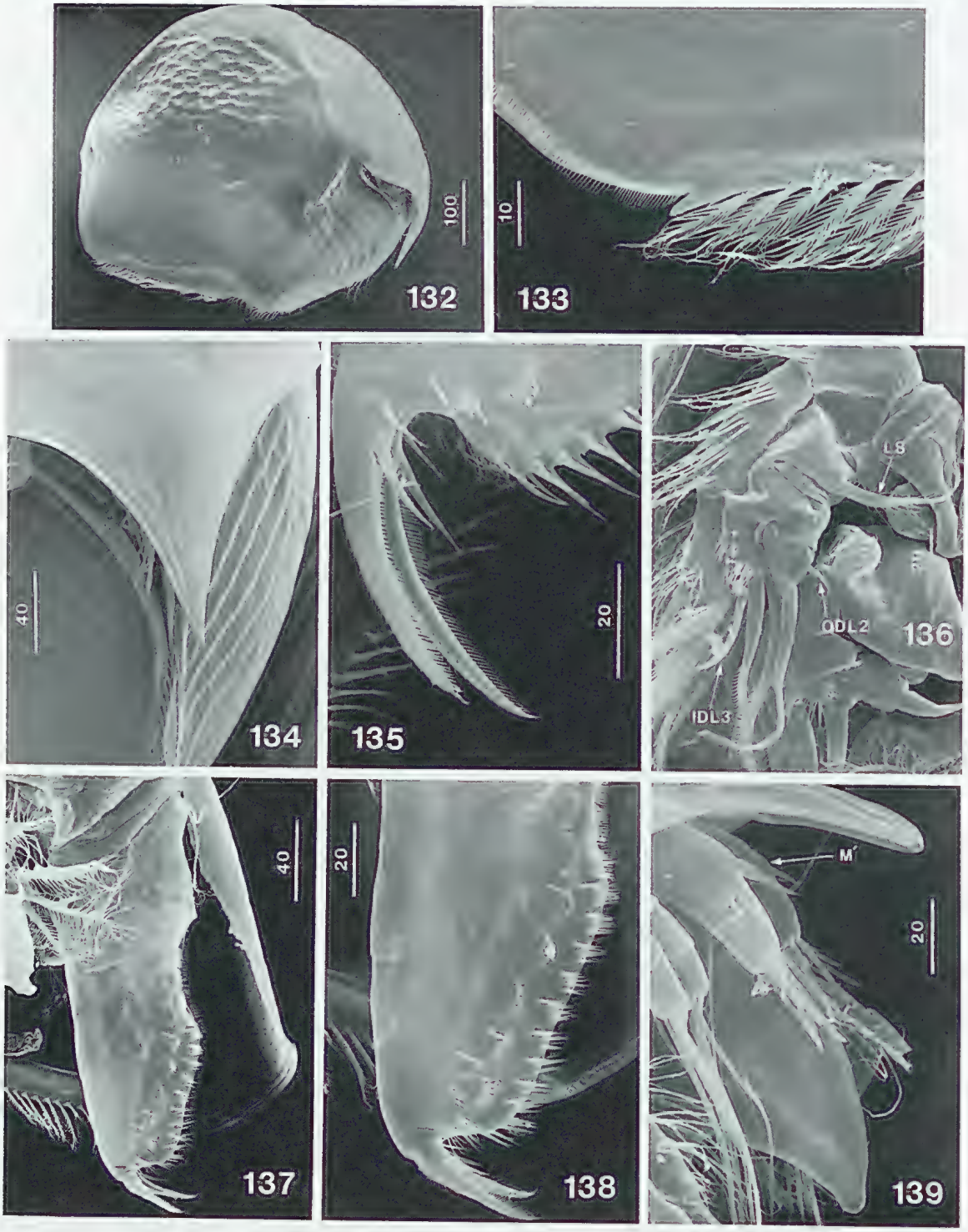
All the remaining specimens from Frey samples 7961 and 8026 are in the Frey collection in Bloomington. The other specimens from Sars F4139 have been returned to the Zoology Museum in Oslo.

**Diagnosis.** Diagnosis and description are based mainly on sample 7961 because of the large number of specimens and the presence of all stages and instars. Any appreciable differences in morphology of specimens from Frey 8026 or Sars F4139 are mentioned. The specimens in Sars F4139 were difficult to dissect for details of head appendages and trunklimb morphology.




**Figs 124-131.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 8026 (natural pond near Waroona, WA, 20 Nov. 1986). 124. instar-II male; 125. mature male; 126. rostrum of instar-II male; 127. rostrum of mature male; 128. postabdomen of instar-II male; 129. postabdomen of mature male; 130. antennule of instar-II male (M', anlage of male seta; AS, antennular seta); 131. antenna of mature male (M, male seta; AS, antennular seta).

Species highly arched dorsally. Posterior margin short, convex. No crest on head or shell. Shell without sculpturing except for about 6-10 short curved striae paralleling anterior margin. Usually no denticle at posterior-ventral angle in Western Australia population, nearly always present in Victoria population, variable in Sars' samples although nearly always present; small, easily overlooked. Well developed seta from basal segment of endopodite of antenna; seta from middle segment as long as distal setae; one of distal seta shorter than other 2; all distal setae of exopodite equally long; terminal spines very short, that of exopodite somewhat longer; spine from basal segment of exopodite very small, sometimes barely visible. Labral keel elongate, narrow, tip narrowly rounded. PP distance three and one half to four times IP distance. Roughly 89 ventral setae




**Figs 132-139.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 7961 (Wellington ferry crossing, River Murray SA, 6 Nov. 1986). 132. ephippial female; 133. medial view of posterior-ventral angle with tooth and of fine setules along posterior margin, parthenogenetic female; 134. rostrum of parthenogenetic female; 135. claw of parthenogenetic female; 136. trunklimb I of parthenogenetic female (LS, lateral seta; ODL2, smaller and unfeathered seta of ODL; IDL3, short seta of IDL); 137, 138, postabdomen of mature male; 139. head end of instar-II male, showing labrum and antennule (M', anlage of male seta).

on shell, including those turned inward at anterior end. Rostrum ending in small rounded point. Postabdomen with preanal portion about equal in length to anal groove, and both considerably shorter than postanal portion; 12-13 marginal denticles, distal ones single, proximal ones with rows of setae proximally; distal half or less of preanal margin single. Postabdominal claw with 2 long, slender basal spines, larger one curved outward and longer than basal width of claw, smaller one slightly shorter. Ephippium with inner shell folded in dimpled fashion and containing some pigment; outer shell essentially without pigment. Rostrum of instar-II male short, broad, tipped with a rounded point; rostrum of instar-III male broadly truncate; antennule of instar-II male with well developed anlage of male seta, which is two thirds length of antennule in mature male but without setation on distal segment. Apparently 2 anlagen of setae at copulatory brush site in instar-II, but could not be resolved in instar-III specimens. Postabdomen of instar-II male very similar to female, of instar-III narrower and with longer postanal portion; claw of mature male shorter and stouter than of female, with 2 basal spines.

**Parthenogenetic female.** *Shell and shape* (Figs 48, 64, 78, 93, 107, 117, 133). Evenly curved dorsally, except for a flattening over headshield in Western Australia specimens. Posterior margin short, only one third total height, evenly convex. Ventral margin with weak bulge in front of middle, essentially straight behind this; provided with about 89 setae (range 82-97, n=40), all marginal except 8-10 most anterior setae, which are strongly submarginal and point posteriorly; setae on anterior half of shell arise from expanded bases. No sculpturing on shell except for about 6-10 short, curved striae anteriorly; these bend posteriorly and continue as 1-3 elongate striae closely paralleling ventral margin. Posterior-ventral angle with single minute denticle in Victoria sample, usually no tooth at all in Western Australia sample, and variable in Sars' samples. No keel on head or shell; body narrow, top rounded in frontal view.

*Head* (Figs 81, 103, 134). Although no keel present, difficult to get headshield to spread out because of extensive curvature from front to rear and from side to side. Rostrum short, tapers to a rounded point that almost seems to be stuck on separately. Somewhat constricted posteriorly and rounded. PP distance three and one half to four times IP distance (about 53-59 µm in mature females); minor pores very small, less than 1 pore diameter apart. No sculpturing of any kind visible under phase optics.

*Antennule* (Figs 63, 78, 108, 120). Elongate, tapered distally, evenly curved. Short, rounded, posterior expansion at base. Nine aesthetascs, all arising from terminal portion, longest almost half length of antennule. Antennular seta arises two thirds from end, almost as long as longest aesthetasc.

*Antenna* (Figs 50, 109, 120, 147). Formula: 0(1)-0-3(1)/1-1-3(1). Terminal setae of exopodite all long, one of endopodite considerably shorter and thinner than other 2. Setae from basal and middle segments of endopodite both well developed, that from middle segment as long as any terminal setae, that from basal segment half again as long as basal segment of middle or terminal setae. All 3 spines short, that of exopodite slightly longer than that of endopodite; spine from basal segment minute and sometimes not distinguishable.

*Labrum* (Figs 55-62, 69-75, 95-102, 120, 139). Elongate, narrow. Anterior margin convex, often with slight concavity near tip. Posterior margin long, irregularly concave. Posterior angle quite sharp, less than 90°. Tip of labrum usually narrow, rounded.

*Trunklimb I* (Figs 49, 67, 136). ODL with 2 setae, smallest of which is short, unfeathered; IDL with 3 setae. Two long IDL setae in typical fashion with row of setules on distal segment. Lateral seta well developed. Middle seta of middle group of corm setae much the longest.

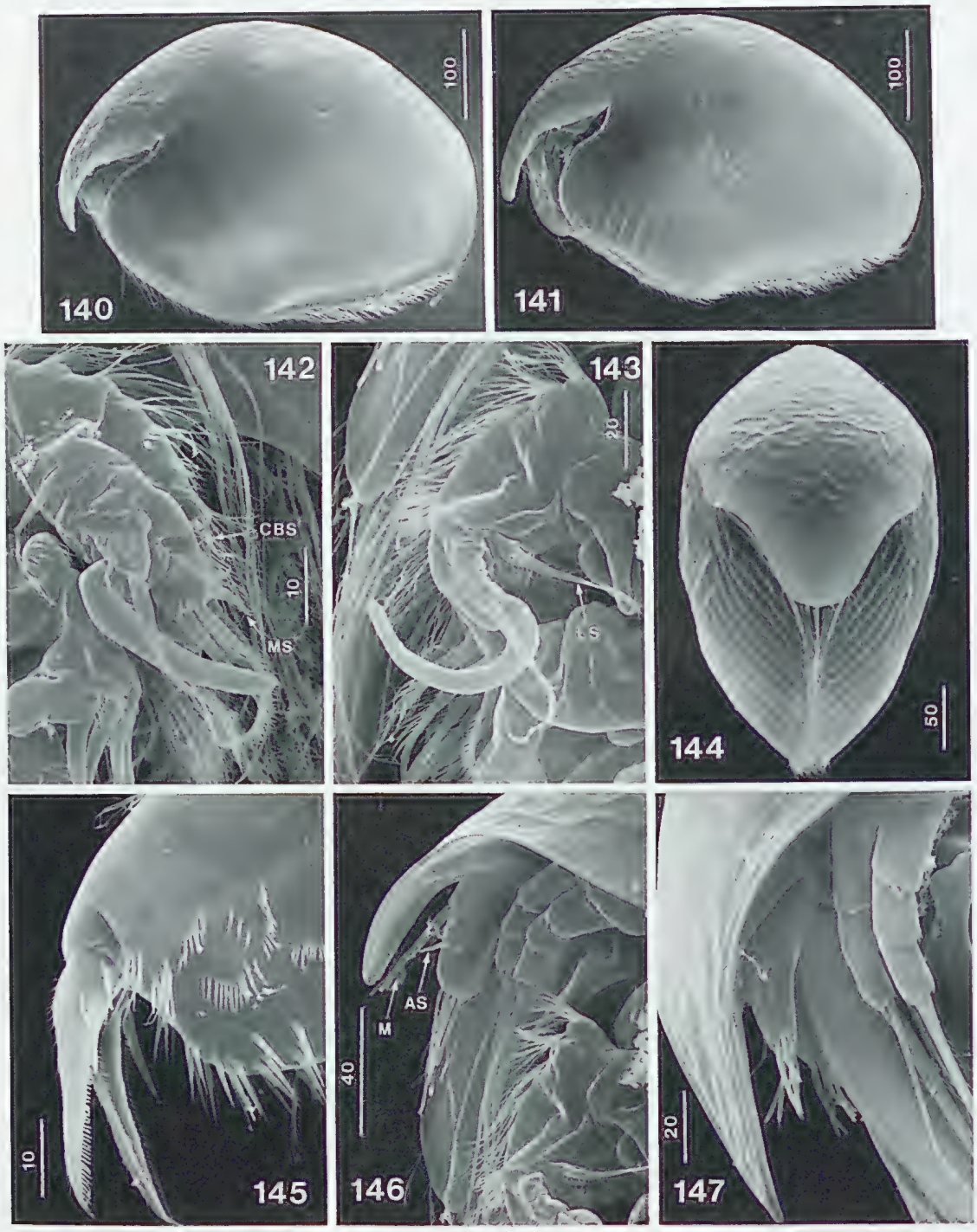
*Trunklimbs II-V* (Fig.68). Setae in gnathobasic filter comb number 8, 8, 6 and 4, respectively. Feathered setae on exopodite 0, 7, 7 and 4, respectively. On trunklimb II, first 4 scraping spines shorter than number 5, all provided with row of very fine setules along distal segment.

*Postabdomen* (Figs 51-53, 76, 104, 105, 121-123, 135). Elongate; postanal margin weakly convex, tapering strongly to distal angle, rounded at tip. Preanal and anal segments about same length, each somewhat shorter than postanal portion. Postanal segment with about 12 straight, slender marginal denticles, distal ones all single, several proximal ones with row of spinules proximally. Anal groove with 4-6 successive rows of slender fringing spinules. Lateral surface with row of setular crescents along postanal portion, 2 rows along much of anal groove, 3 transverse rows at preanal angle and anterior to it. Ventral margin with 2 transverse crescents of fine setules. Distal half of preanal portion a single ridge with several weak diagonal furrows, proximal half more complex because of infolding and expansion. Abdominal setae somewhat longer than preanal segment.

*Postabdominal claw* (Figs 54, 77, 106, 123, 135). Long; both margins evenly curved. Concave margin provided with two sequential rows of fine setules. Two well developed but slender basal spines, distal one longer than basal width of claw, distinctly curved away from claw, proximal one straight, slightly shorter than width of claw.

**Ephippial female** (Figs 66, 82, 94, 118, 119, 132). Slightly more compressed from side to side than parthenogenetic female (cf. Figs 93 and 94, 117 and 118), hence headshield more elongate and attenuated posteriorly (Fig.82). Inner shell of ephippium lightly pigmented, outer shell unpigmented. On moulting, anterior-ventral portions of shell peel away from ephippium but remain attached posteriorly (Figs 66, 119). Inner shell pulls in around single ephippial egg, producing dimpled surface pattern dorsally (Fig.66). Other details of morphology as in parthenogenetic female.

**Male.** Body much less high than in female (Figs 79, 80, 110-112, 124, 125, 140, 141). Rostrum of all 3 instars shorter than in female so that even in instar-I some aesthetascs extend beyond tip; rostrum of instar-II broad, short, tapered to small knob-like structure at tip (Figs 84, 113,126); rostrum of instar-III broadly truncate, with rounded lateral angles (Figs 83, 85, 114, 127,144). Antennule of male broader than in female but with same rounded backward-projecting diverticulum at base; instar-II has well developed anlage of male seta (Figs 87, 130, 139); instar-III with this fully developed, but without any brush-like setation of distal segment (Figs




**Figs 140-147.** *Pleuroxus inermis* Sars, 1896. All specimens are from Frey sample 7961 (Wellington ferry crossing, River Murray, SA, 6 Nov. 1986). 140. instar-II male; 141. mature male; 142. trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta); 143. trunklimb I of mature male (LS, lateral seta); 144. frontal view of mature male (note that the top is rounded, without a ridge or keel); 145. distal end of postabdomen and postabdominal claws of mature male; 146. head end of mature male, showing antennule, antenna, labrum, and part of trunklimb I (M, male seta; AS, antennular seta); 147. head end of parthenogenetic female, showing antennule (note posterior expansion at base) and antenna.

86, 131, 141, 146); antennular seta arises one third to one quarter from tip, closer to tip in instar-III; instar-III definitely has 12 aesthetascs as counted from their places of attachment as seen in terminal view. Trunklimb I shows typical changes in copulatory hook morphology from peg-like tooth in instar-I (Figs 79, 110) to well-developed U-shaped hook in instar-III (Figs 88-90, 142, 143), with the free limb very slender and with 3 rounded bumps (or crescents) near tip. Instar-II has 2 anlagen of setae at the site of the copulatory brush seta (Fig.88), the larger of which will become the copulatory brush seta in the next instar. Neither could be recognised with high-power phase in instar-III. Postabdomen of instar-I (Figs 79, 110) with postanal portion short, as in instar-I female, bordered by about 13 short slender denticles; ventral margin frequently irregular distally; genital pores not visible. Postabdomen of instar-II much the same as in female, except for waviness of ventral margin (Figs 92, 115, 128); genital pore slightly lateral and some distance from tip. Postabdomen of instar-III narrowed (Figs 91, 116, 129, 137, 138, 145), and postanal portion more elongate than in female; in Western Australia specimens, marginal denticles in proximal half are terminal member of transversely or diagonally oriented crescents (Figs 91, 129); South Australia specimens have more denticles distally, some doubled, and smaller crescents or rows proximally (Figs 116, 137, 138, 145); postabdominal claw shorter and stouter than in female, but still with 2 basal spines (Figs 91, 116, 138, 145).

**Length.** Western Australia (Frey 8026). Overall 0.30-0.57 mm (n=221). Females: instar-I 0.31-0.37 mm (n=88); instar-II 0.38-0.43 mm (n=26); mature 0.45-0.57 mm (n=49); smallest with eggs 0.45 mm; ephippial 0.47-0.55 (n=7). Males: Instar-I 0.30-0.36 mm (n=44); instar-II 0.38-0.40 mm (n=5); mature 0.40-0.43 mm (n=2).

South Australia (Frey 7961). Overall 0.33-0.63 (n=235). Females: instar-I 0.33-0.39 mm (n=54); instar-II 0.41-0.47 mm (n=40); mature 0.47-0.62 mm (n=95); smallest with eggs 0.47 mm; ephippial 0.54-0.63 mm (n=12). Males: Instar-I 0.34-0.37 mm (n=3); instar-II 0.41-0.46 mm (n=25); mature 0.45-0.47 (n=6).

New South Wales (Sars F4139). Overall 0.34-0.60 (n=199). Females: Instar-I 0.34-0.36 mm (n=3); instar-II 0.41-0.42 mm (n=6); mature 0.44-0.60 mm (n=190); smallest with eggs 0.44 mm.

**Comments.** These three populations are very similar but exhibit some differences, the significance of which is not yet understood. Thus, the various stages and instars in Frey 7961 are uniformly larger than the corresponding stages and instars of Frey 8026 (Fig.1). Frey 7961 has a slightly longer IP distance and a slightly shorter PP distance, yielding a PP/IP ratio averaging 3.3 instead of 3.8 as in Frey 8026 (Table 1). Frey 7961 has a single small tooth on the shell, which is only rarely absent, whereas Frey 8026 lacks a tooth in nearly all specimens, only occasionally having a single small tooth on one valve. In Sars F4139, 59% of 179 mature individuals had a single tooth on both valves, 20% a single tooth on one valve only, and 21% had no tooth. In addition, specimens from Sars F4139 have a longer secondary seta on the ODL than the other two populations. As already stated, such differences may have resulted from isolation of these populations from one another for some considerable period of time.

Of the various species of *Pleuroxus* seen in Australia, *P. inermis* seems the one most likely to be confused with *P. aduncus*. But although the females are vaguely similar, the mature males are not. This emphasises once again the fact that males are really needed to establish species and their limits and to decipher relationships between species.

The major differences in morphology between *Pleuroxus aduncus sensu stricto* from Denmark and *Pleuroxus inermis* from Australia are given in Table 3.

### ***Pleuroxus hastirostris*** Sars

Figs 148-172

*Pleuroxus hastirostris* Sars, 1903: 635, figs 8, 8a-c.–Deevey, 1955: 302-303, figs 3-4,10-12,31.–Smirnov, 1971: 225, fig.207.

**Remarks.** Sars had only several parthenogenetic females from a collection from D'Urville Island, New Zealand, none of which are still extant. He considered that it resembled the Australian *P. inermis*, but that it lacked curved striae on the anterior part of the shell and it had a small but distinct tooth at the posterior-ventral angle. Deevey (1955) found abundant remains of *P. hastirostris* in sediments from Pyramid Valley on South Island, and Smirnov (1971) had material from a pond at Silverdale. Deevey's paper is non-taxonomic, although he makes some comments about the similarity of *P. hastirostris* to *P. inermis* and possibly to *P. aduncus*. His drawings of remains include an ephippium. Smirnov's (1971) description is based mainly on Sars (1903), and he copied Sars' three illustrations of the species. I have found the taxon in only one of the 157 samples I collected in New Zealand. In addition, V.M. Stout had specimens in her samples 12 and 84 from South Island. All available specimens are parthenogenetic females except for one male from the Frey sample. The species has not been reported from any other region and hence seems to be endemic to New Zealand.

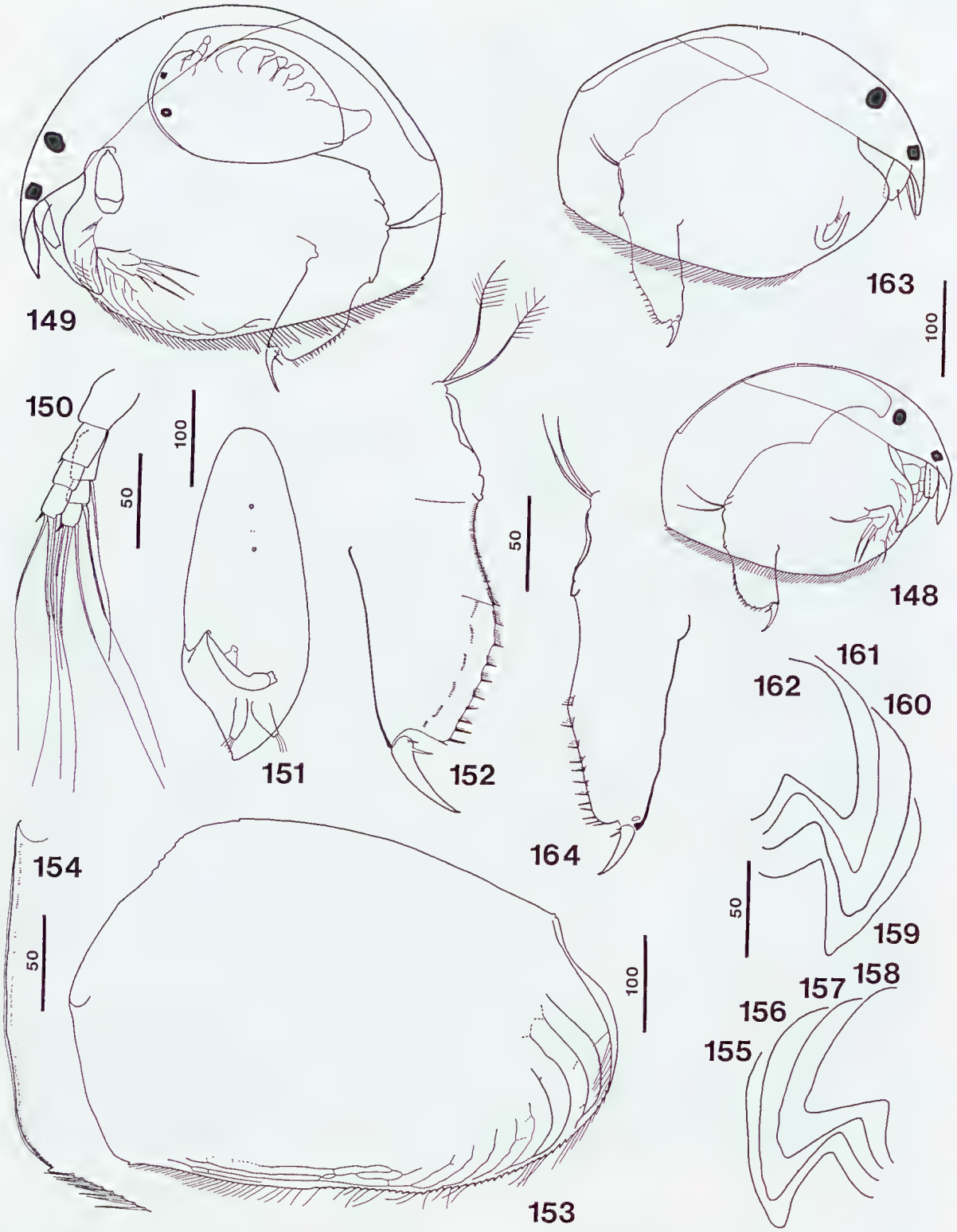
**Material examined.** 1. Frey 8388 from Lake Waihola, south of Dunedin, 23 Mar. 1987, collected by D.G. Frey. Yielded 235 specimens, including one male.

2. Sample 12 from Rush Swamp off Pyramid, 29 Nov. 1964, collected by V.M. Stout. Yielded 5 parthenogenetic females. Stout has 4 samples from this locality, 2 each from 29 Nov. and 13 Dec. 1964.

3. Sample 84 from a farm pond between Oamaru and Timaru, 29 Aug. 1961, collected by V.M. Stout. Yielded 27 parthenogenetic females.

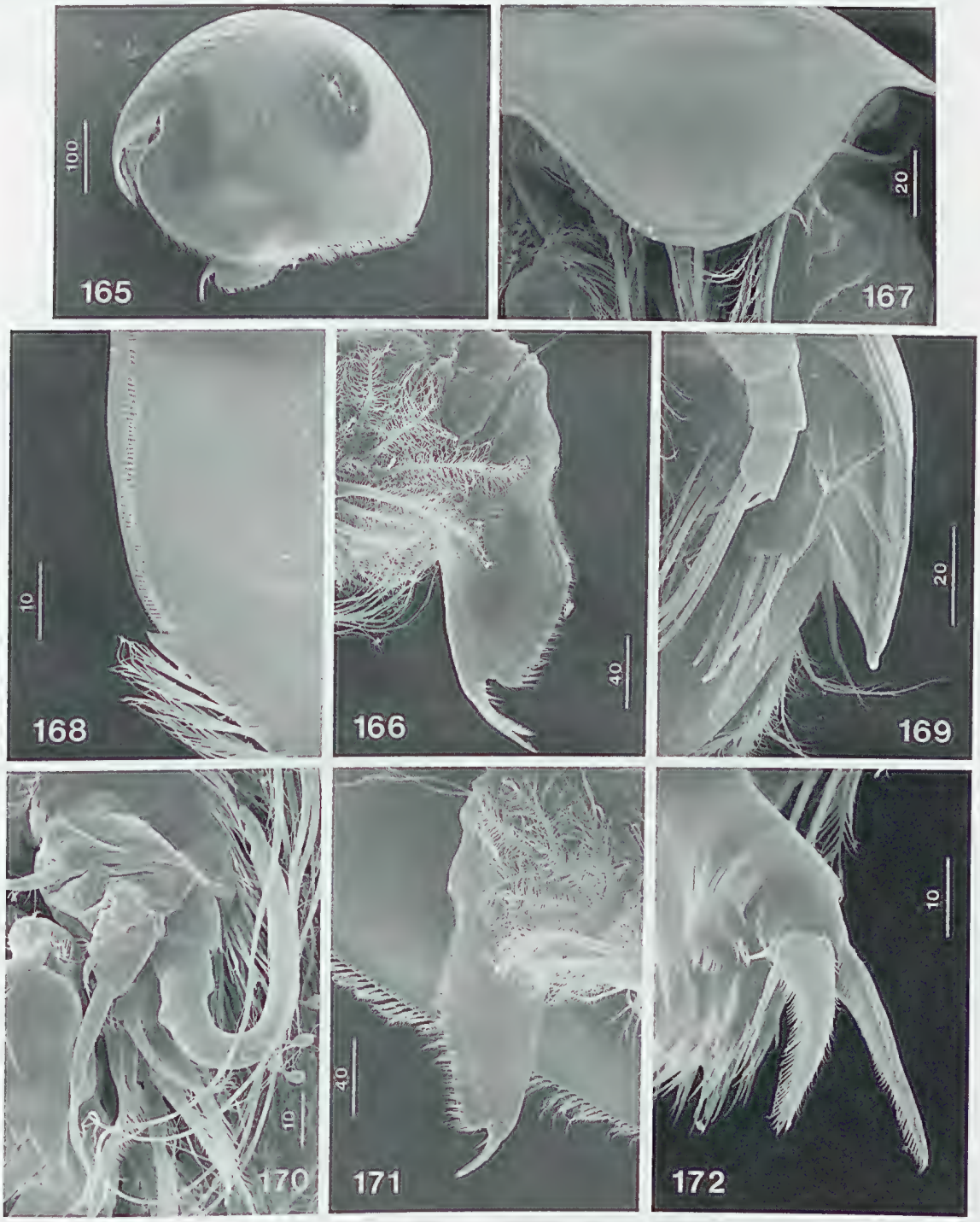
**Disposition of specimens.** One parthenogenetic female, mounted on a slide in glycerine jelly, has been deposited in each of the following museums: AM (P39463), NMNZ (Cr.6422), BM(NH) (1989.609), USNMNH (242117). All the other specimens from Frey 8388 plus the specimens in Stout's samples 12 and 84 are in the Frey collection in Bloomington.

**Diagnosis.** Body considerably longer than high; dorsal margin evenly rounded from rostrum to posterior-dorsal angle, which is indistinct; posterior margin short, evenly but weakly convex; single small but distinct tooth




**Figs 148-164.** *Pleuroxus hastirostris* Sars, 1903. All specimens from Frey sample 8388 (Lake Waihola near Dunedin, NZ, 23 Mar. 1987). 148. instar-I female; 149. parthenogenetic female; 150. antenna of parthenogenetic female; 151. headshield of parthenogenetic female; 152. postabdomen of parthenogenetic female; 153. shell of parthenogenetic female; 154. posterior-ventral angle and posterior margin of shell of parthenogenetic female; 155-162. labra; 163. mature male; 164. postabdomen of mature male.

at posterior-ventral angle; ventral margin moderately bulged anterior to middle; about 8 or 9 short, faint striae paralleling anterior margin, no keel on head or shell. PP distance about 2.6 times IP distance in mature females; rostrum short and broad, ending in rounded point. Postabdomen tapers evenly from postanal angle, provided with about 8-10 long, slender denticles, nearly all of which have accessory setae associated with them; proximal denticles with long rows of long setae oriented obliquely to margin; single row of spinular crescents laterally; distalmost third of preanal portion single and with a couple of transverse ridges bearing rows of setae; anterior two thirds expanded laterally. Postabdominal claw with a row of setae along concave margin, a row of long thin setae along medial surface, and a sparse, ragged row of thin setae along convex margin; 2 basal




**Figs 165-172.** *Pleuroxus hastirostris* Sars, 1903. All specimens from Frey sample 8388 (Lake Waihola near Dunedin, NZ, 23 Mar. 1987). 165. parthenogenetic female; 166. postabdomen of parthenogenetic female; 167. rostrum of mature male; 168. inside view of posterior-ventral angle of shell and of setation along posterior margin of mature male; 169. dissected head end of mature male (M, male seta; AS, antennular seta); 170. trunklimb I of mature male (ODL2, smaller seta of ODL, showing slight feathering; MS, male seta); 171, 172. postabdomen and claws of mature male.

spines, distal one long and curved away from claw, proximal one straight and only about half as long. Male much less high than female; postabdomen narrower than in female, tapered distally from postanal angle, provided with about 9 rows of long setae oriented obliquely to margin; genital pore just above base of claw; postabdominal claw shorter than in female and with longer setae along concave margin; male seta on antennule long, tapered to sharp tip, without any feathering; antennular seta arises slightly distal of male seta; rostrum shortened, broadly rounded, with small tubercle medially, which is tucked underneath; tip of copulatory hook with 3 bumps near tip of concave margin; smaller seta on ODL well developed and weakly feathered terminally.

**Parthenogenetic female.** *Shape and shell* (Figs 148, 149, 153, 154, 165, 168). Dorsal margin highly and evenly rounded, with no concavity near posterior-dorsal angle; no keel on head or shell; ventral margin weakly bulged ventrally anterior to middle, with continuous row of 78 (range 74-81, n=8) marginal setae. Anterior-ventral portion of shell with 8 or 9 short, faint striae, curving parallel to anterior margin, and continuing posteriorly as 1-3 straight striae close to and paralleling ventral margin (Fig.153), with very few cross connections; vague, short lines, like ridges, on shell, but no other markings except irregular polygonal ridges from contraction. Small but distinct and sharply pointed tooth just anterior to posterior-ventral angle, followed posteriorly by submarginal row of fine setae that continue to posterior-dorsal angle at somewhat greater distance from margin.

*Head* (Figs 149, 151). Rostrum short, broad, ending in rounded point; tip curving somewhat posteriorly, held away from body; IP distance 56 (range 54-59 µm, n=6); PP/IP ratio 2.6. No keel behind headpores. Posterior margin rather broadly rounded. Eye oval, oriented transverse to margin; ocellus somewhat smaller; both almost touching margin.

*Antennule*. Elongate, rather slender, tapering distally. Nine aesthetascs, about one third to one half length of antennule. Antennular seta about one third from tip.

*Antenna* (Figs 150, 169). Formula: 0(1)-0-3(1)/1-1-3(1). Terminal setae of exopodite all long; one terminal seta from endopodite shorter, scarcely more than half length of other 2; seta from middle segment as long as terminal setae, that from basal segment well developed but only about half as long. Both terminal spines and spine from basal segment of exopodite very small.

*Labrum* (Figs 149, 155-162). Broad, short; irregularly convex anteriorly, weakly concave posteriorly; attenuated to broad, rounded tip; posterior angle moderately sharp, less than 90°.

*Trunklimbs I-V*. Few details observable; middle seta of middle group on limb I longest; gnathobasic filter setae 8, 6 and 4, respectively, on limbs III, IV and V; exopodite feathered setae 7,7 and 4 on limbs III, IV and V, respectively.

*Postabdomen* (Figs 152, 166). Preanal and anal portions about equal in length, both less than postanal portion; latter tapers almost in straight line to rounded distal angle. Margin of preanal portion single in distal third with a couple of rounded transverse rolls; margin of proximal two thirds double from lateral expansion. 8-10 long, slender marginal denticles, each accompanied by up to 6 or even more long setae, those in middle clusters arranged somewhat obliquely. Single row of crescents of spinules parallels dorsal margin along lateral surface, with more complicated arrangement around preanal angle. Preanal angle reasonably distinct, postanal angle broadly rounded. Abdominal setae short, not reaching middle of anal groove when extended. Two crescents of fine spinules across ventral margin.

*Postabdominal claw* (Figs 152, 166). Long, slender, with hook-like bending at tip; continuous row of well-developed setae along concave margin to tip, another similar row along medial surface, third row of more slender seta along convex margin, giving ragged appearance. Two basal spines: distal one somewhat longer than basal width of claw, curved away from claw, proximal one only about half as long and straight.

**Male** (Figs 163, 164, 167, 169-172). The single specimen found was first drawn with the light microscope, then used for SEMs. Body elongate; shell anterior to ventral bulge slopes upward more strongly than in female and turns inward, thereby obscuring marginal setae. Rostrum short, broadly rounded, provided with small, bulb-like tip, which is recurved, partially obscured (Fig.169). Antennule broader than in female (Figs 163, 169). Male seta of antennule long, slender, tapering to fine point; arises about two fifths from tip (Fig.169); antennular seta arises slightly distal from here, very slender, tapering; seemingly only 9 aesthetascs, although these are always difficult to count. On trunklimb I, copulatory hook irregular at base, then tapers smoothly to narrow tip with 3 knobs on concave surface (Fig.170); smaller ODL seta well developed and feathered distally; male seta on IDL tapered gradually to sharp point, curved forward in direction of copulatory hook; lateral seta well developed; copulatory brush somewhat confused in SEM, and copulatory-brush seta not readily visible. Postabdomen narrower than in female (compare Figs 152 and 164, 166 and 171), tapers gradually from postanal angle to rounded tip distally; provided with about 9 short rows of long setae, oriented obliquely to dorsal margin (Fig.171), all about same size and hence difficult to designate any one as a denticle; lateral crescents of spinules, and 2 of small spinules across ventral edge, as in female; genital pores far distad, near base of claws (Fig.172). Postabdominal claws shorter than in female; setae along concave margin longer, and longer basal spine not so strongly curved, otherwise much the same.

**Length.** Lake Waihola females: overall 0.28-0.50 mm (n=234); instar-I 0.28-0.34 mm (n=62); instar-II 0.35-0.39 mm (n=112); smallest female with eggs 0.40 mm; male 0.39 (n=1). Stout sample 12: parthenogenetic females 0.46-0.52 mm (n=5). Stout sample 84:

parthenogenetic females 0.50-0.63 mm (n=27).

**Comments.** The considerable discrepancy in length of specimens between the Frey population and the two Stout populations suggested the possibility of two different species. However, all the Stout specimens agree closely in morphology with the Frey specimens, and, moreover, the shell drawn from Frey sample 8388 is much larger than that of any of the intact individuals collected, indicating that the maximum size of the taxon is considerably greater than suggested by the specimens in the sample.

### *Pleuroxus foveatus* n.sp.

Figs 173-257

**Etymology.** From (L) *fovea*, a small pit, referring to the many small dimples covering the surface of the shell.

**Comments.** The four populations representing this species are all from south-western Western Australia, two from the general region of Esperance and two from the Lake Muir region 400 km to the west. Hence, unlike a number of other species here reported that to now are known only from single localities, this taxon is quite widely distributed at least in Western Australia. Three of the four localities had conductivities between 3000 and 7000 µS $cm^{-1}$, indicating inland brackish water. Many of the waterbodies in this general region are endorheic and intermittent, and consequently would be expected to have variable salinity depending on their hydrologic phase. This particular species seems adapted to such conditions.

Three of the populations are very similar to one another, but the fourth is slightly different. A tabulation of some of the characteristics of each population is given below to indicate the extent of these differences.

| | Length range | 1st | Gnathobasic filter combs | | | | IP length | | Shell setae | |
|---|---|---|---|---|---|---|---|---|---|---|
| Population | (mm) | eggs | II | III | IV | V | (µm) | PP/IP | Mean | Range |
| Shiel 857 | 0.38-0.71 | 0.51 | 8 | 9(8) | 6 | 4 | 47 | 6.2 | 102 | 94-108 |
| Shiel 856 | 0.40-0.65 | - | 8 | 9 | 6 | 4 | 46 | 6.4 | 101 | 93-106 |
| Bayly 51 | 0.41-0.65 | 0.53 | 8 | 9 | 6 | 4 | 53 | 5.8 | 100 | 89-107 |
| Shiel 839 | 0.35-0.65 | 0.49 | 8 | 8(9) | 6 | 4 | 55 | 4.7 | 102 | 100-113 |

One of the distinctive characteristics of this taxon is nine setae in the gnathobasic filter comb of trunklimb III, but there is some variation. Thus, the type population had six limbs with nine setae and two with eight, and Shiel 839 had four with eight setae and two with nine. The latter population also has a slightly greater IP distance and a considerably smaller PP/IP ratio. The population available also seemed somewhat smaller, and first eggs occurred in smaller females (Fig.1). The PP distance is a problem, because it is measured as the chord distance in intact specimens. Hence, a greater curvature posterior to the pores could lead to a somewhat smaller ratio, although not to the seemingly significant reduction in ratio in Shiel 839. Other characteristics of this population, though, are quite concordant with the other three populations, so that (for the moment at least) it is considered to belong to the same taxon. Perhaps it represents the magnitude of differentiation that can occur among semi-isolated populations in these marginal waterbodies in Western Australia.

**Material examined.** *Type locality.* Flooded margin of Lake Muir, 50 km south-east of Manjimup, WA, collected 8 Oct. 1981 by R.J. Shiel, his accession number 857 (field number W.A. 67). The water at the time of sample collection was shallow, black and humic, and with a conductivity of 7000 µS $cm^{-1}$. The sample yielded 283 specimens, including abundant ephippial females and all three instars of males.

*Other localities.* (1) Small interconnecting channel between Lake Muir and Cowerup Swamp, located about 50 km south-east of Manjimup, WA, collected 8 Oct. 1981 by R.J. Shiel, his accession number 856 (field number W.A. 66). The water at this time was listed as black and peaty; conductivity 3500 µS $cm^{-1}$. The sample yielded 16 individuals, including 5 males distributed among the three instars. (2) Shark Lake, 11.2 km north of Esperance, WA, collected 6 Oct. 1981 by R.J. Shiel, his accession number 839 (field number W.A. 48). The water was shallow, the bottom muddy, conductivity 3000 µS $cm^{-1}$. The sample yielded 106 individuals, including 2 ephippial females and 3 mature males. Ostracods were the dominant organisms. (3) A roadside pond, 87 km west of Esperance on road to Ravensthorpe, WA, collected 27 June 1980 by I.A.E. Bayly, his sample 51. The sample yielded 35 specimens, all parthenogenetic females.

**Types.** HOLOTYPE – a parthenogenetic female 0.54 mm long, mounted on a slide in glycerine jelly, AM (P39464). ALLOTYPE – a mature male 0.47 mm long, mounted on a slide in glycerine jelly, AM (P39465). Special PARATYPES – 1 individual each of the following stages and instars, mounted separately on 2 slides in glycerine jelly, AM: an ephippial female 0.64 mm long (P39468), an instar-I male 0.39 mm long (P39467), and an instar-II male 0.45 mm long (P39466). PARATYPES – 1 slide each of a parthenogenetic female, an ephippial female, an instar-II male, and a mature male, all mounted

in glycerine jelly, have been placed in several museums, as listed below. The numbers given are the catalogue or registration numbers of the specimens.

| | AM | NZNM | BM(NH) | USNMNH |
|---|---|---|---|---|
| Shiel 857: PARATYPES | | | | |
| parthenogenetic female | – | Cr. 6423 | 1989.610 | 242118 |
| ephippial female | – | Cr. 6424 | 1989.612 | 212118 |
| instar-II male | – | Cr. 6425 | 1989.613 | 242118 |
| mature male | – | Cr. 6426 | 1989.611 | 242118 |
| Shiel 839 | | | | |
| parthenogenetic female | P39469 | Cr. 6427 | 1989.614 | 242119 |
| ephippial female | P39470 | – | – | – |
| mature male | P39471 | – | – | – |
| Bayly 51 | | | | |
| parthenogenetic female | P39472 | Cr. 6428 | 1989.615 | 242120 |

All the remaining paratypes and specimens from Shiel 856, 839, and Bayly 51 are in the Frey collection in Bloomington.

**Diagnosis.** Parthenogenetic female almost as high as long; median ridge on head behind pores and on shell; about 10 short curved striae anteriorly, roughly paralleling anterior margin, ventral tips uniting and continuing posteriorly as 1 or 2 longitudinal striae; small triangular tooth at posterior-ventral angle, followed along posterior margin by row of submarginal setules; entire surface of shell and of head behind pores dimpled; roughly 100 ventral setae, including about 10 at anterior end directed inward. Rostrum rather long, tapered to finely rounded, weakly offset tip; IP distance about 46-55 µm, PP distance 4.7-6.4 times IP distance. Antennule elongate, rather thin, tapered distally to small aesthetasc field, not surrounded by triangular points; 9 aesthetascs, one of which arises subterminally outside aesthetasc field; antennular seta arises about two fifths from end, about four fifths as long as antennule; backward projecting rounded extension at base. Antenna with 8 long swimming setae, one from basal segment of endopodite and one from each terminal group of three somewhat shorter than others. Labrum with elongate, narrow tip, convex anteriorly except for slight concavity near tip; posterior margin concave; posterior angle less than 90°, narrow. Trunklimb I with short second seta on ODL not feathered; middle seta of middle group of corm setae longest. Gnathobasic filter combs of trunklimbs II-V have 8, 9, 6 and 4 setae, respectively; exopodites of limbs III-V have 7, 7 and 4 feathered setae, respectively. Postabdomen with preanal and anal portions subequal, both shorter than postanal; about 13-15 long, slender marginal denticles, single distally but with 1 or more subdenticles or setae proximally; single row of spinular crescents along postanal and most of anal portions; several transverse rows in preanal region. Postabdominal claw weakly curved, concave border with 2 sequential rows of long setae; longer basal spine slender, curved, longer than basal width of claw; shorter basal spine about half as long. Body without pigmentation, only slight yellowish hyaline tinge. Ephippial female with 1 resting egg; lining of brood pouch darkly pigmented; shell in ephippial region more darkly hyalinised, with dimples and small tubercles; slough line proceeds to ventral margin, so that shell flaps easily lost on moulting. Good anlage of male seta on antennule in instar-II; postabdomens and claws of instar-I and instar-II males similar to females of these instars, except for genital pores and the irregular ventral margin in instar-II. Mature male has long, simple male seta on antennule, possibly only 9 aesthetascs; rostrum short, broadly rounded; postabdomen more elongate and more slender than in female, but marginal and lateral armament similar; genital pore near base of claw; postabdominal claw shorter, but otherwise resembles that of female.

**Parthenogenetic female.** *Shape and shell* (Figs 173, 174, 187, 199, 209-213, 242, 253). Body high, but not quite so high as long; uniformly curved from tip of rostrum to posterior-ventral angle, with only slight change in curvature at posterior-dorsal angle. Posterior margin weakly convex, with heavy line following closely submarginally. Ventral margin with mean of 102 setae (range 89-113, n=53), including about 10 setae anteriorly that bend inward instead of projecting away from body; setae of anterior third relatively unfeathered, those in posterior two thirds strongly feathered; each seta attached to a triangular swelling at base, producing weak serrate appearance. 10-15 short, curved striae at anterior end, roughly paralleling anterior margin, longest anteriorly, becoming progressively shorter posteriorly; shell striae fuse together ventrally and continue posteriorly as 1 or 2 striae closely paralleling ventral margin; some suggestions of meshes posteriorly (Figs 199, 212, 235, 237, 238), but not defined by any striae; entire shell and head posterior to pores covered by small dimples, but no other markings. Small triangular tooth at posterior-ventral angle (Figs 187, 242), occasionally absent or occasionally 2 teeth, followed by submarginal row of small setules along posterior margin to posterior-dorsal angle. Body laterally compressed. Shell clear, without pigmentation.

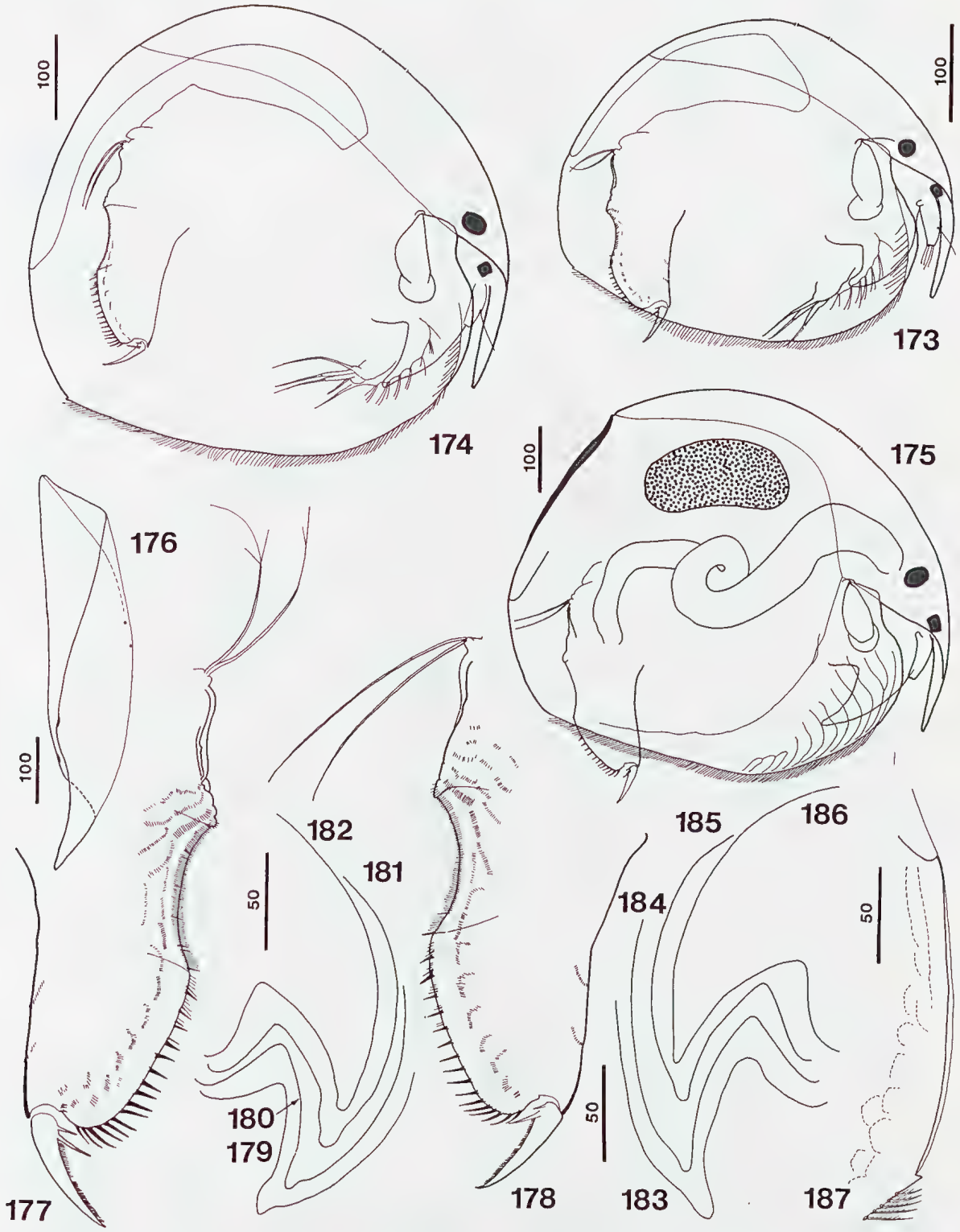
*Head* (Figs 221-223, 239). Weak median ridge from behind pores to posterior-dorsal angle (Figs 240, 241). IP distance of mature females 46-55 µm (n=24), PP distance (chord distance of whole specimens) 4.7-6.2 times IP; of males IP 42 µm (n=4), PP distance 4.3 times IP. Minor pores about one pore diameter apart. Rostrum long, tapering to finely rounded tip that is weakly demarcated from rest of rostrum (Fig.239). Ocellus roughly quadrangular in shape; eye somewhat larger, ovoid, oriented with long axis perpendicular to dorsal margin; ocellus one third distance from eye to tip of rostrum. Head behind pores with fine dimples; anterior portion smooth.

*Antennule* (Figs 189, 222). Elongate, quite narrow, tapered distally; backward projecting rounded tubercle at base. Antennular seta about four fifths length of antennule, arising from prominent annulus about two fifths from tip. Nine aesthetascs, one of which seems to arise subterminally outside aesthetasc field; all

subequal in length. Aesthetasc field not surrounded by pyramidal points.

*Antenna* (Fig.223). Formula: 0(1)-0-3(1)/1-1-3(1). Eight long swimming setae; seta from basal segment of endopodite more than two thirds as long as terminal setae, and 1 terminal seta on each ramus somewhat shorter than other 2. Terminal spines short, about one third as long as segments to which attached; spine from basal segment of exopodite very short, delicate.

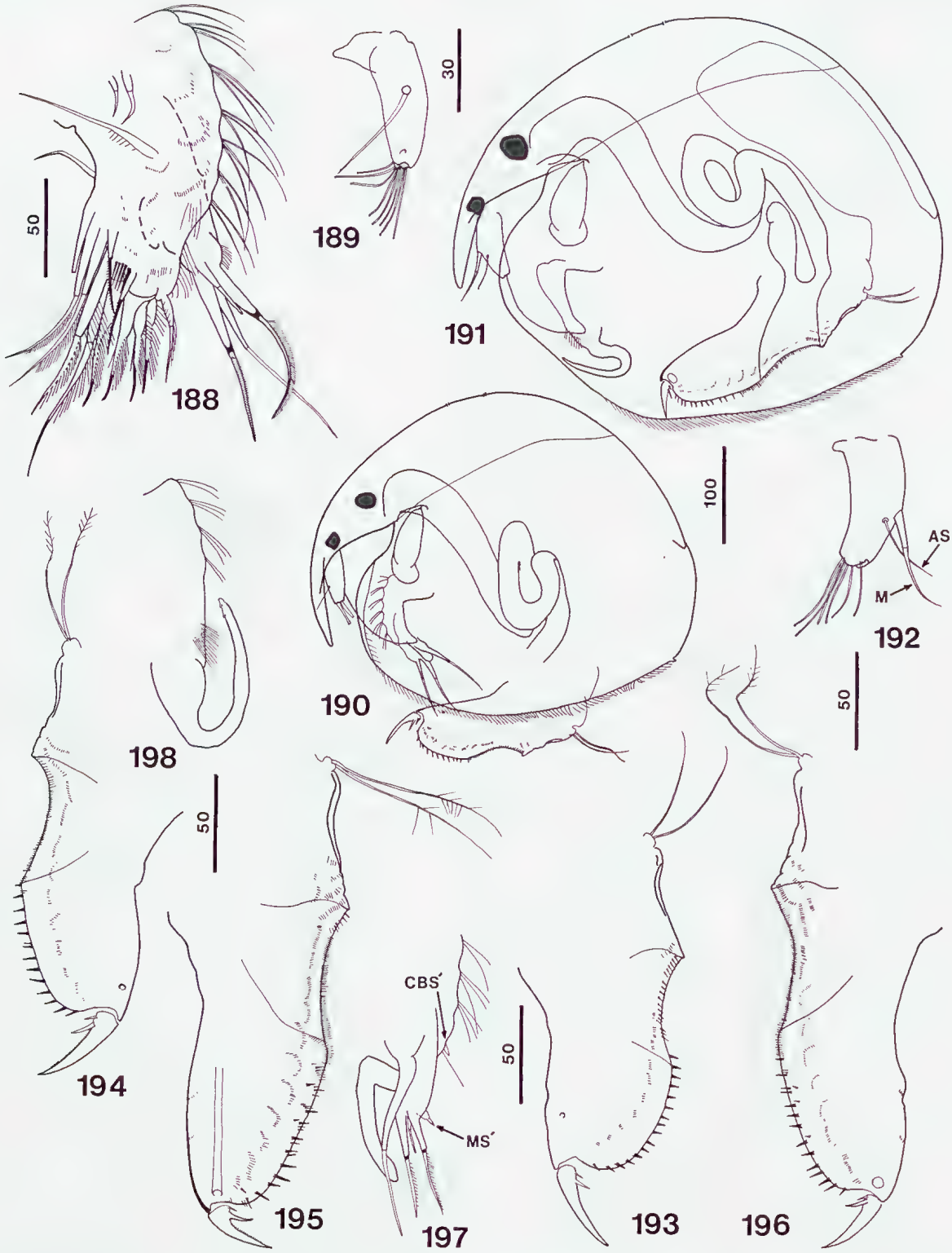
*Labrum* (Figs 179-186, 214-219). Ventral tip elongate, narrow; anterior margin usually evenly convex except for slight concavity or waviness near tip; posterior



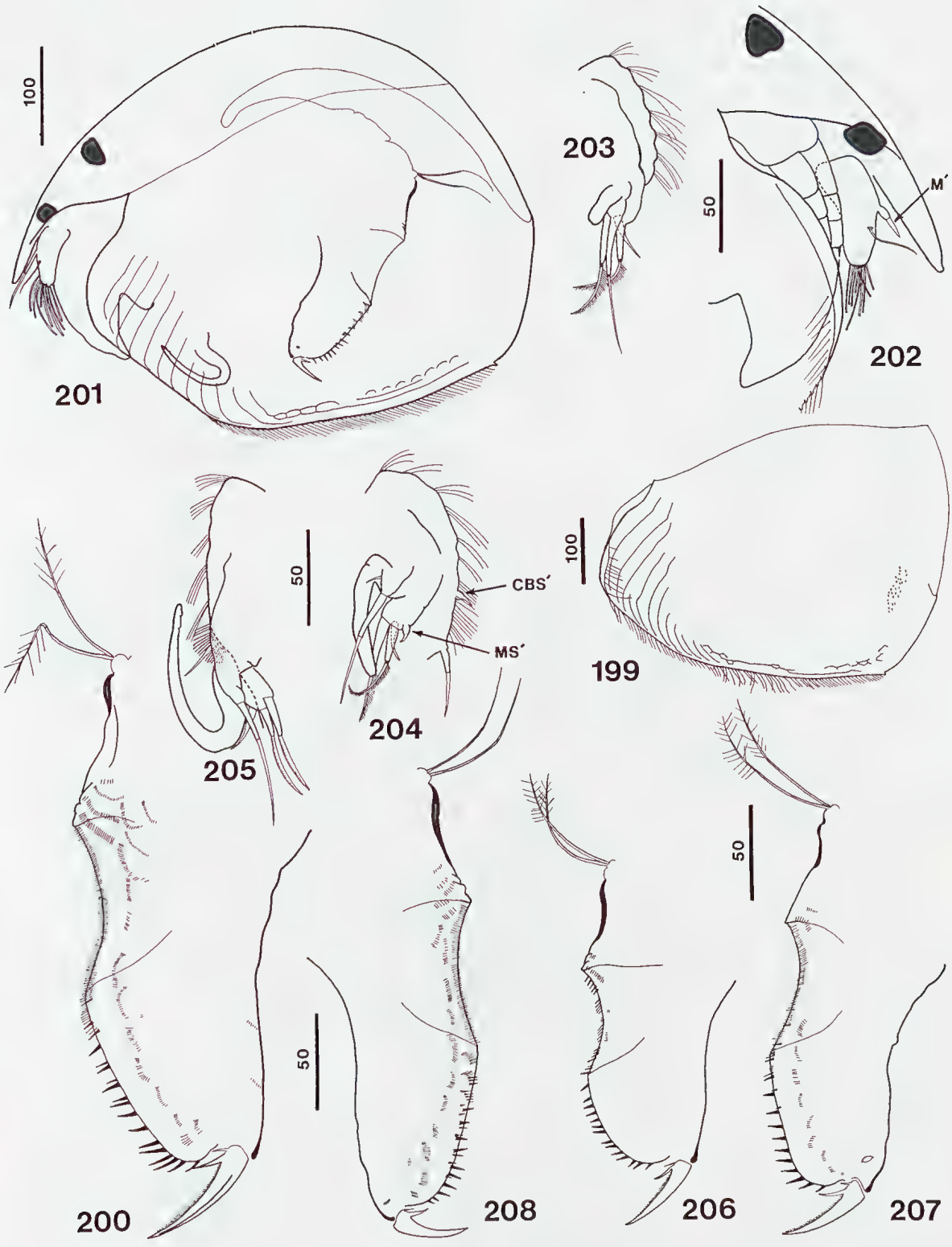

**Figs 173-187.** *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 173. instar-I female; 174. parthenogenetic female; 175. ephippial female; 176. headshield of parthenogenetic female; 177, 178. postabdomen of parthenogenetic female; 179-186. labra; 187. posterior-ventral angle and posterior margin of shell of parthenogenetic female.

margin irregularly concave; posterior angle narrow and less than 90°.

*Trunklimb I* (Figs 188, 224, 225, 254). ODL with 2 setae, 1 very short, unfeathered (Fig.254). IDL with 3 setae, 1 of which is short, stout to the tip, and about as long as basal segment of other 2, seemingly without any marginal setules; 2 long IDL setae with fringe of long, fine setules along distal segment (Fig.254). Middle seta of middle group of corm setae longest. Lateral seta from base of ODL-IDL ridge long, well developed,



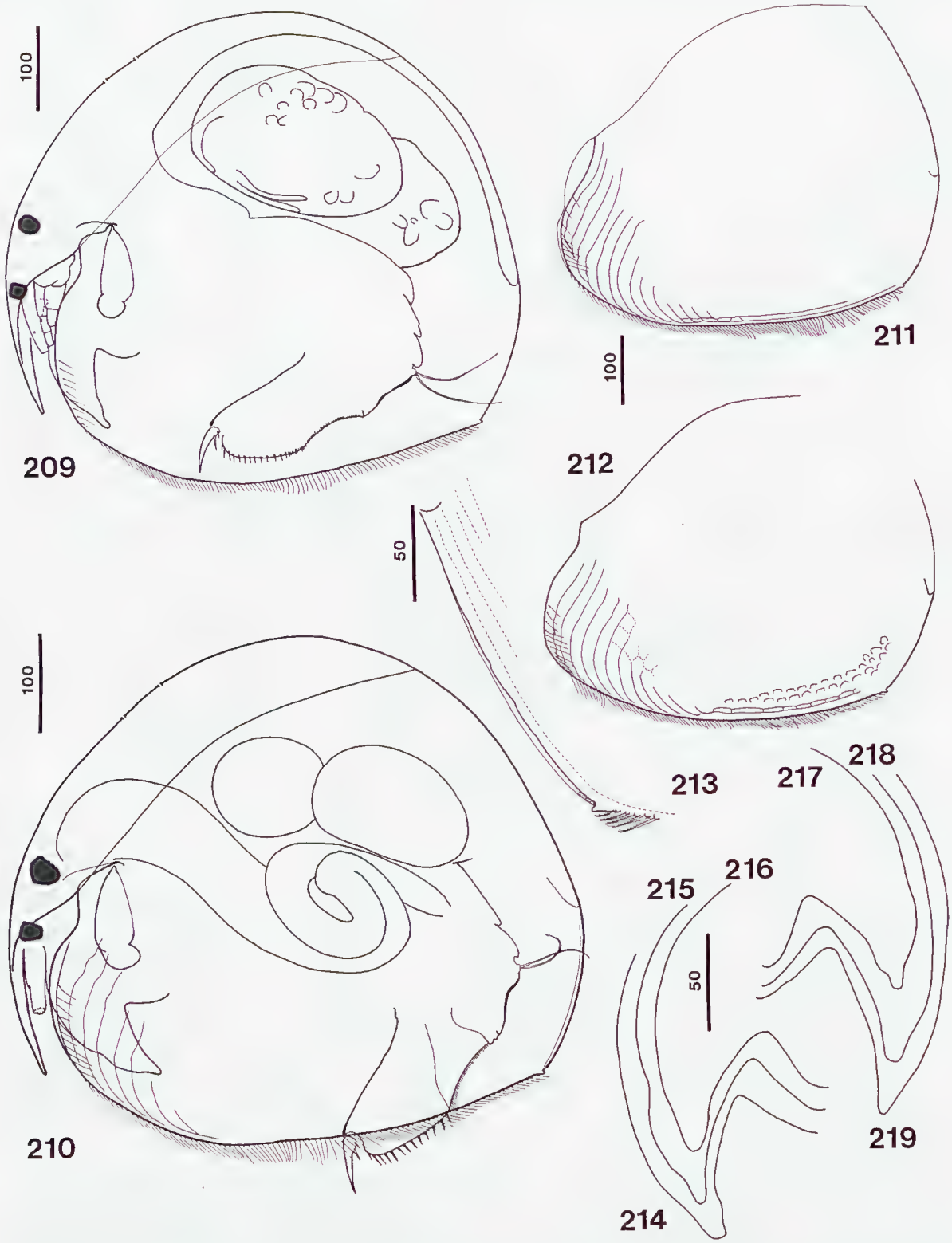

**Figs 188-198.** *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 188. trunklimb I of parthenogenetic female; 189. antennule of parthenogenetic female; 190. instar-I male; 191. mature male; 192. antennule of mature male (M, male seta, unfeathered; AS, antennular seta); 193. postabdomen of instar-I male; 194. postabdomen of instar-II male; 195, 196. postabdomen of mature male; 197. trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 198. copulatory hook of mature male.




**Figs 199-208.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 856 (interconnecting channel between Lake Muir and Cowerup Swamp, WA, 8 Oct. 1981). 199. shell of parthenogenetic female, showing distribution and size of a few dimples near posterior end; 200. postabdomen of parthenogenetic female; 201. mature male (note unequal lengths of aesthetascs and irregularity of ventral margin of postabdomen); 202. head end of instar-II male (M', anlage of male seta); 203. part of trunklimb I of instar-I male; 204. part of trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta of IDL); 205. part of trunklimb I of mature male (CBS, copulatory brush seta; MS, male seta of IDL); 206. postabdomen of instar-I male (note shortness of postanal region and few, coarse setae along anal groove); 207. postabdomen of instar-II male; 208. postabdomen of mature male.

brush-like in distal two thirds.

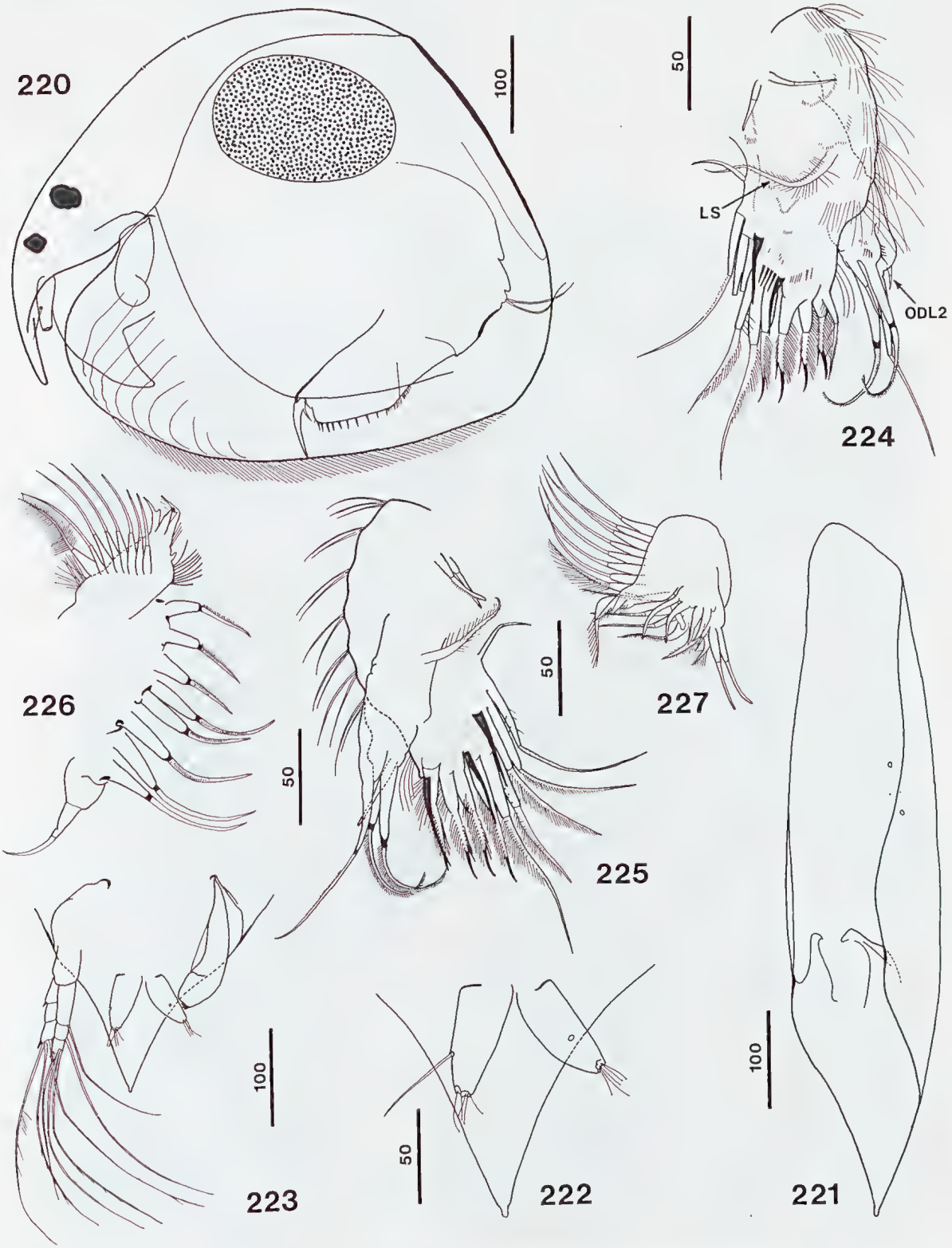
*Trunklimbs II-V* (Figs 226, 227). Setae in gnathobasic filter comb 8, 9, 6 and 4 on limbs II-V, respectively; feathered exopodite setae 7, 7 and 4 on limbs III-V, respectively. On trunklimb II (Fig.226), margin between gnathobasic setae and scraping spines contains 2 or 3 setae close to gnathobase, often obscured by it, then a blunt broad seta or denticle, followed by an average of 7 (range 5-10, n=12) thick setae curved toward gnathobase, tips of proximal ones coarsely frayed; scraping spines 1-3 subequal in length, 4-6 subequal and longer, and 7-8 subequal and still longer, all provided




**Figs 209-219.** *Pleuroxus foveatus* n.sp. Specimens 210, 211, and 213-219 from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981); specimens 209 and 212 from Bayly sample 51 (roadside pond west of Esperance, WA, 27 June 1980). 209, 210. parthenogenetic female; 211, 212. shell of parthenogenetic female; 213. posterior margin of shell and posterior-ventral angle of parthenogenetic female; 214-219. labra of parthenogenetic females.

with very fine setulation along distal segment.

*Postabdomen* (Figs 177, 178, 200, 230-233, 255). Anal groove equal to or slightly shorter than preanal portion, both considerably shorter than postanal portion. Preanal portion with 3 or 4 weak scallops in margin distally. Postanal portion with 13-15 long, slender marginal denticles, arising close together distally, further apart proximally; distal denticles single, proximal denticles with subdenticles and setae. Anal groove with about 5 sequential rows of fine setae that project well beyond margin. Lateral surface with row of crescentic clusters of spinules, generally 2 rows along anal groove,

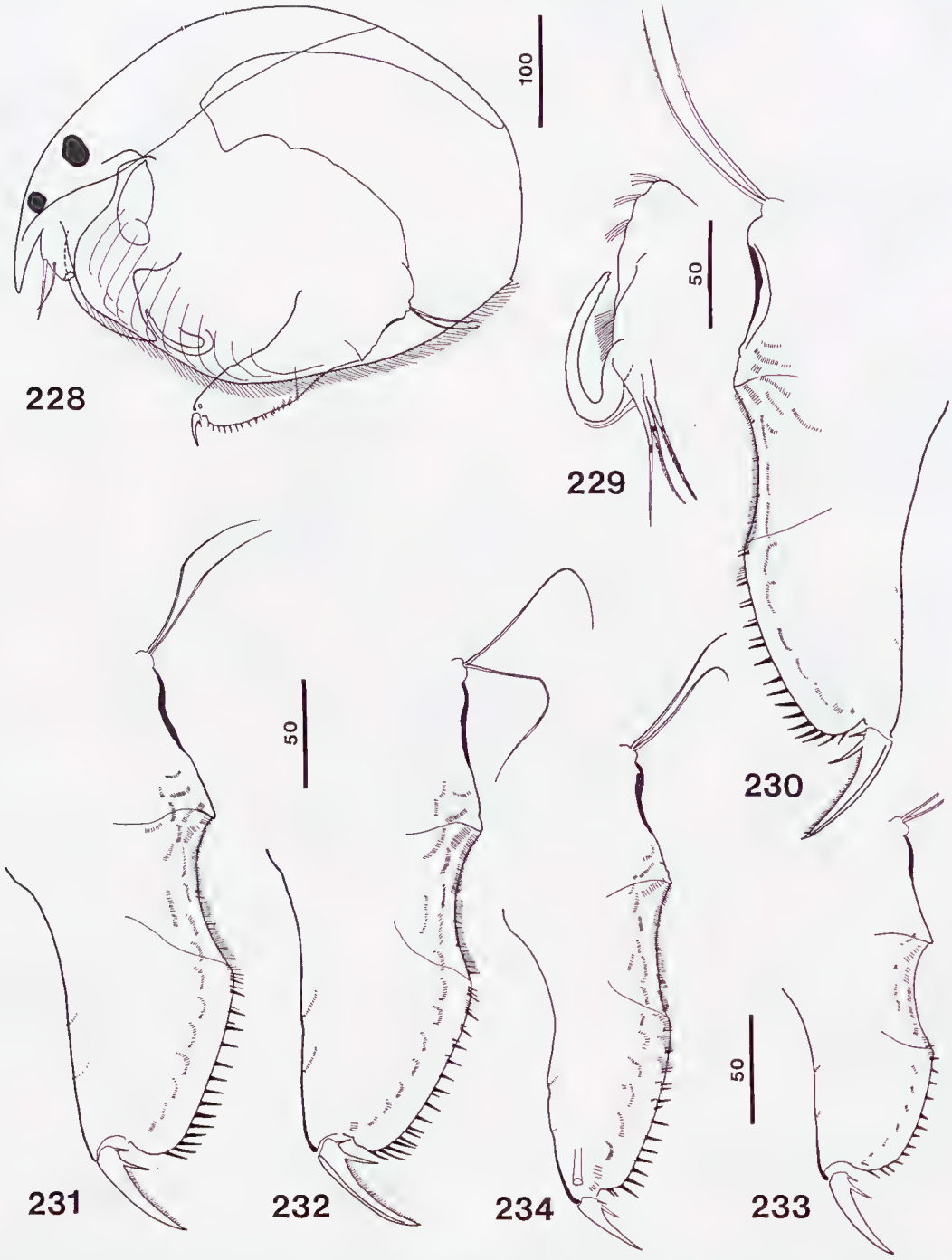



**Figs 220-227.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981). 220. ephippial female; 221. headshield of parthenogenetic female; 222, 223, rostrum, antennules, and antenna of parthenogenetic female (note small size of spines on antenna); 224, 225. trunklimb I of parthenogenetic female (LS, lateral seta; ODL2, shorter ODL seta, not feathered); 226. trunklimb II of parthenogenetic female; 227. gnathobasic portion of trunklimb III of parthenogenetic female.

up to 4 or 5 rows roughly perpendicular to preanal margin. Ventral margin not expanded basally; 2 crescents of fine spinules across ventral margin. Abdominal setae about one and one third times as long as preanal margin.

*Postabdominal claw* (Figs 177, 178, 200, 230, 255). Both dorsal and ventral margins weakly but evenly curved; concave margin with 2 sequential rows of long setae, those in distal row slightly longer. Both basal spines slender, evenly tapered and curved away from claw; longer one longer than basal width of claw, shorter one less than basal width.

**Ephippial female** (Figs 175, 220, 235, 236, 251-253). Headshield much narrowed posteriorly, with weak triangular expansion opposite sloughline (Fig.251). Slough line evidenced by lines and irregular meshes, indicating where breakage will occur; extends to marginal patch of irregular meshes in front of posterior-ventral angle, so that ephippium easily loses shell flaps completely but retains tooth and about 7-10 setae anterior to it. Sculpturing over ephippium a sequence of large dimples and small granules (Figs 236, 252). Pigmentation of broodpouch lining heavy, with darker hyalinisation of ephippial surface; sometimes difficult to



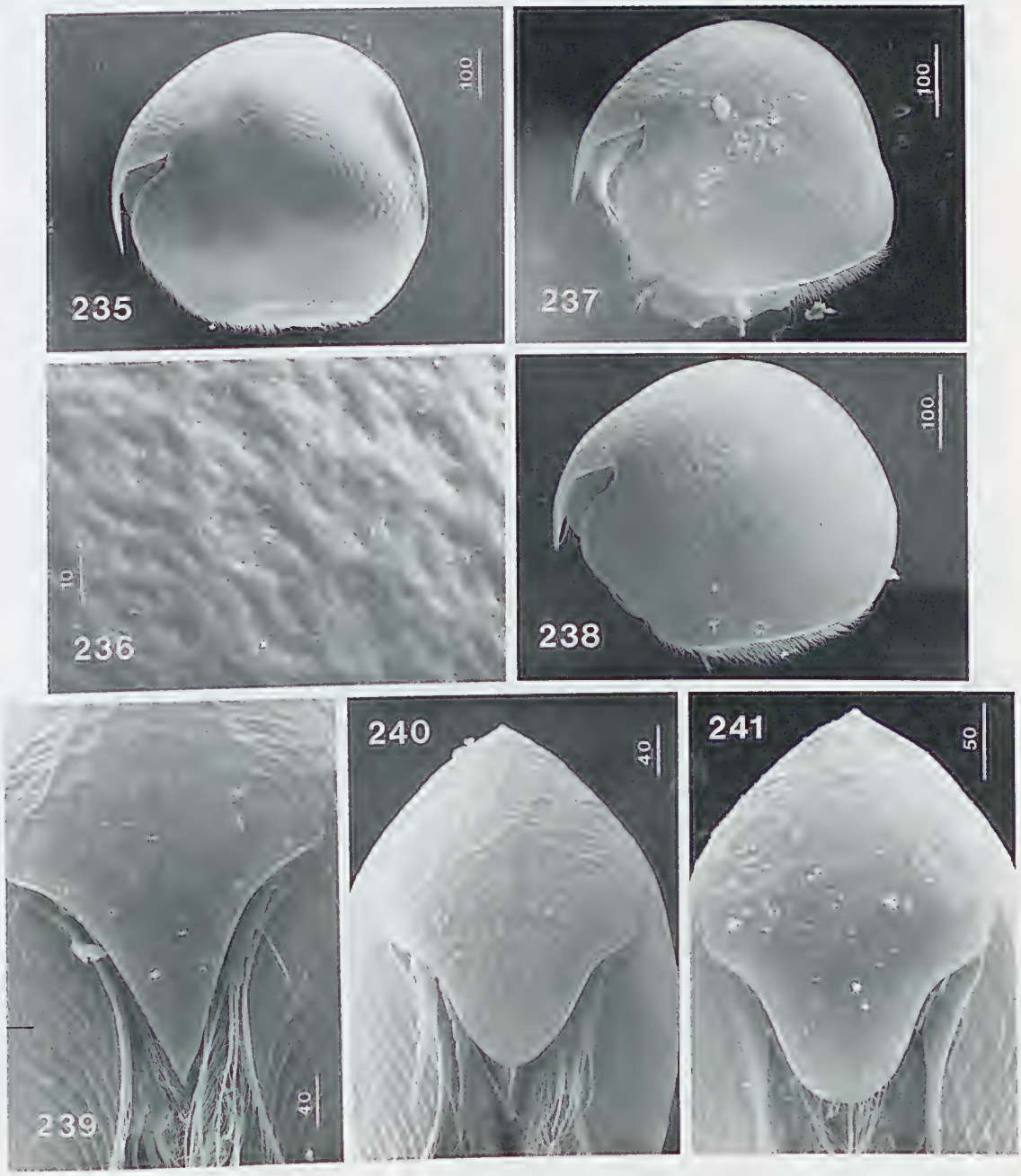

**Figs 228-234.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981). 228. mature male (note the good development of both the male seta and the antennular seta); 229. part of trunklimb I of mature male; 230-232. postabdomen of parthenogenetic female; 233. postabdomen of instar-I female; 234. postabdomen of mature male.

see ephippial egg; rest of animal unpigmented. Heavy chitinous thickening along dorsal margin of shell, occasionally a notch or angle in contour where shell and head join on midline posteriorly (Figs 175, 220, 235).

**Male.** *Instar-I* (Figs 190, 193, 203, 206). Rostrum somewhat shorter than in female; aesthetascs reach tip. Trunklimb I with short finger-like anlage of copulatory hook. Postabdomen similar to that of instar-I female (compare Fig.233 with 193 and 206) with shortened postanal portion and a few rather coarse setae in groups along anal groove, all pointing distally; genital pore small, located some distance from end (Fig.193).

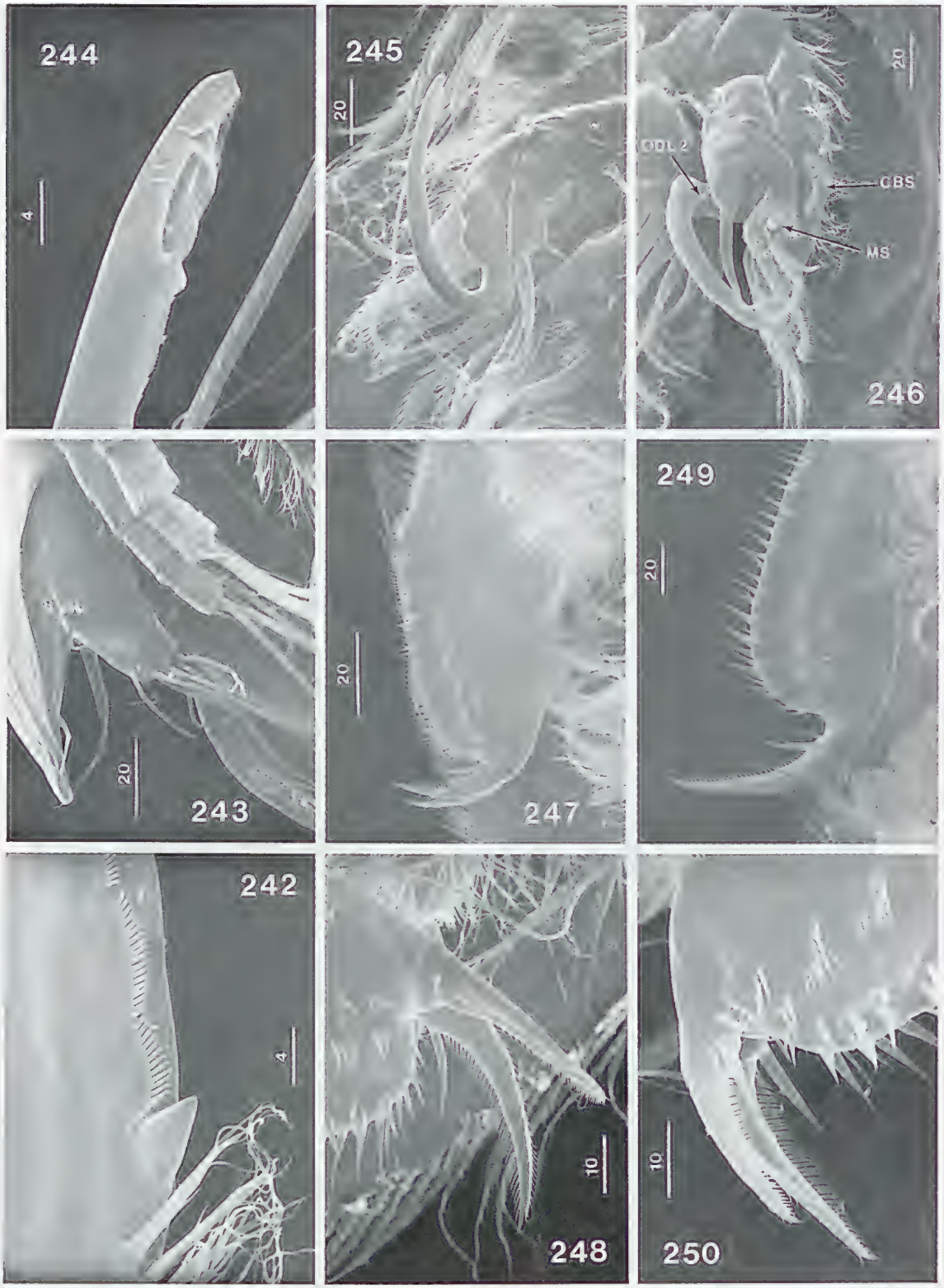
*Instar-II* (Figs 194, 197, 202, 204, 207, 237, 240, 246-248). Rostrum still somewhat shorter (Fig.240); aesthetascs far exceed tip. Antennule with conspicuous anlage of male seta (Fig.202). Trunklimb I with J-shaped anlage of copulatory hook directed posteriorly, and with anlagen of male seta and copulatory brush seta. Postabdomen similar to instar-II female, except that ventral margin more irregular; genital pore has shifted more distally from its position in instar-I.

*Mature* (Figs 191, 192, 195, 196, 198, 201, 205, 208, 228, 234, 238, 241-245, 249, 250, 256, 257). Rostrum short, broadly rounded (Fig.241). Antennule with 2-segmented male seta, consisting of very long basal segment with little taper and apical segment without lateral setules (Figs 191, 192, 201, 243); seta about as




**Figs 235-241.** *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 235. ephippial female; 236. patterning of shell of ephippial female, showing dimples; 237. instar-II male; 238. mature male; 239. rostrum of parthenogenetic female; 240. front view of instar-II male, showing especially ridge on top of shell and shape of rostrum; 241. similar view of mature male.

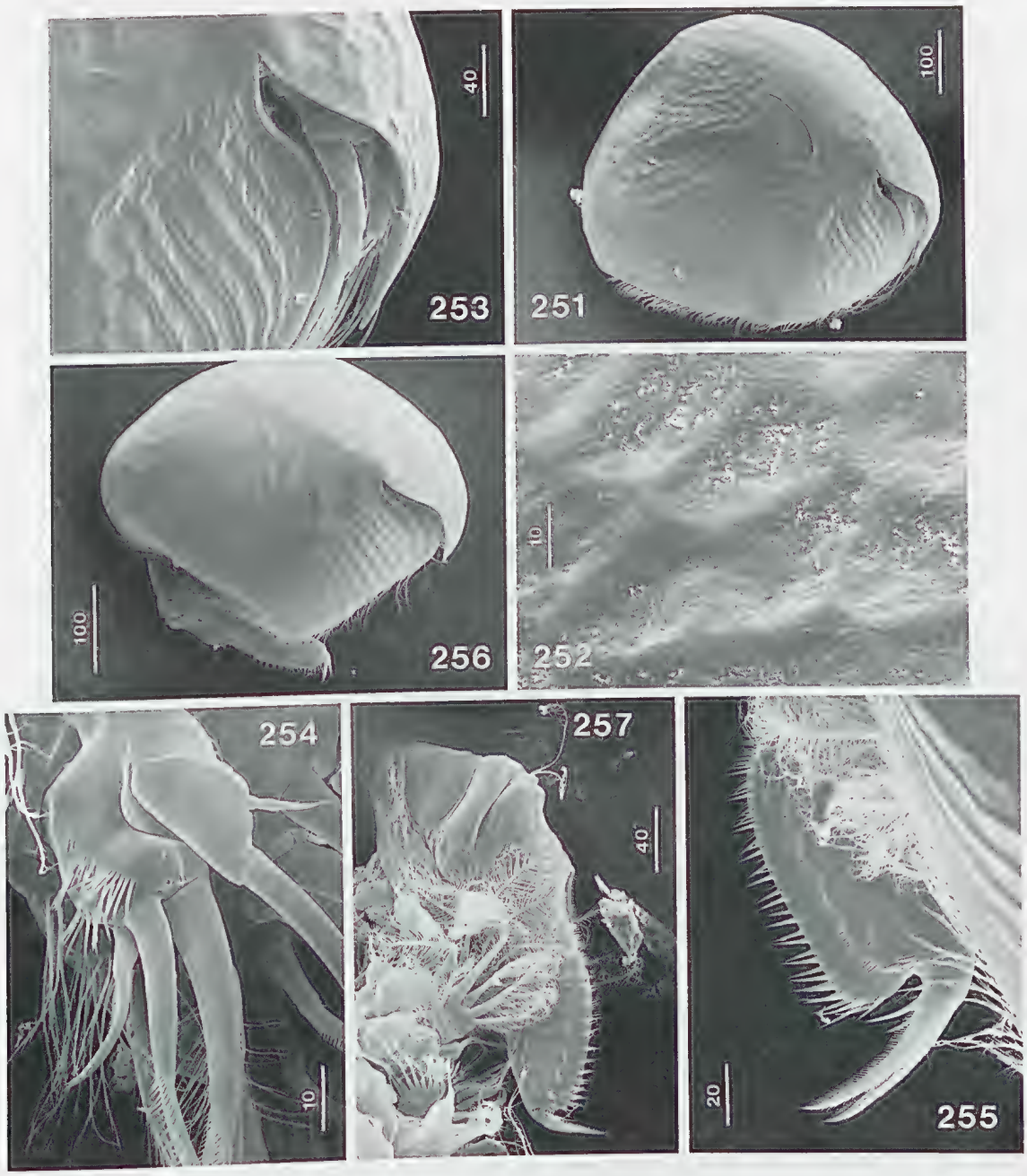
long as antennule, arising about midway; antennular seta almost as long, arising slightly more distally; seemingly only 9 aesthetascs, but difficult to count; antennule reaches tip of rostrum. Trunklimb I with well-developed male seta on IDL curving forward parallel to copulatory hook; copulatory brush seta largely hidden within copulatory brush; copulatory hook with very slender free branch (Fig.245), having 2 ridges on inside near




**Figs 242-250.** *Pleuroxus foveatus* n.sp. All specimens PARATYPES from Shiel sample 857 (margin of Lake Muir, WA, 8 Oct. 1981). 242. posterior-ventral angle and part of adjacent posterior margin of shell of mature male; 243. antennule and antenna of mature male; 244. tip of copulatory hook of mature male; 245. trunklimb I with copulatory hook of mature male; 246. trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL; ODL2, smaller ODL seta); 247, 248. postabdomen and postabdominal claws of instar-II male; 249, 250. postabdomen and postabdominal claws of mature male.

tip, representing crescentic folds across hook (Fig. 244). Postabdomen elongate and narrowed (Figs 195, 196, 208, 234, 247), but with both anal angles distinct; has essentially same marginal and lateral armament as female; marginal denticles mostly single distally, multiple proximally, the latter arranged as crescents or rows arching away from margin; genital pore near tip and just slightly lateral of ventral midline. Postabdominal claw somewhat shorter than in female but otherwise with similar shape and armament. Anterior-ventral margin of shell straight in side view, coursing upward toward head (Figs 191, 201, 228); edges rolled inward, causing marginal setae to be indistinct.

**Length.** *Type series.* Females: overall 0.38-0.71 mm (n=204); instar-I 0.38-0.44 mm (n=89); instar-II 0.46-0.51 mm (n=32); smallest with eggs 0.51 mm; ephippial 0.58-0.71 mm (n=20). Males: Instar-I 0.37-0.43 mm (n=17), instar-II 0.41-0.48 mm (n=25); mature 0.46-0.54 mm (n=37). *Shiel 856.* Females: overall 0.40-0.65 (n=11); immature (mostly instar-I) 0.40-0.51 mm (n=9). Males: Instar-I 0.41 mm (n=1); instar-II 0.44-0.48 mm (n=2); mature 0.49-0.53 mm (n=2). *Bayly 51.* Females: overall 0.41-0.69 mm (n=35); instar-I 0.41-0.44 mm (n=4); instar-II 0.47-0.51 mm (n=10); smallest with eggs 0.53 mm. *Shiel 839.* Females: overall 0.35-0.65 mm (n=104); instar-I 0.35-0.39 mm (n=11); instar-II 0.40-




**Figs 251-257.** *Pleuroxus foveatus* n.sp. All specimens from Shiel sample 839 (Shark Lake near Esperance, WA, 6 Oct. 1981). 251. ephippial female; 252. surface sculpturing of shell of ephippial female, showing many small dimples; 253. head end of ephippial female; 254. ODL and IDL of trunklimb I of parthenogenetic female (note good size of ODL2, but without any, or only slight, feathering); 255. postabdomen of parthenogenetic female; 256. mature male; 257. postabdomen of mature male.

0.45 mm (n=14); smallest with eggs 0.49 mm. Mature males 0.43-0.47 mm (n=3).

## *Archepleuroxus* Smirnov & Timms

### *Archepleuroxus baylyi* Smirnov & Timms

Figs 258-314

*Archepleuroxus baylyi* Smirnov & Timms, 1983: 21, pl. 20a-i.

**Remarks.** The chief characteristic of this taxon, according to Smirnov & Timms (1983), is that it is polyembryonic, like *Saycia* and the various species of *Eurycercus*. They state that it is very similar in morphology to *Pleuroxus jugosus*, which is scarcely correct, and that it is quite similar to *Saycia*, which it can resemble only grossly. It is very similar to some of the other species of *Pleuroxus*-like forms, particularly those from Western Australia, but it differs so markedly from them, particularly in the structure of the postabdomen, that quite definitely it should be in a different genus.

Smirnov and Timms had the taxon from two localities in Victoria, seven in Tasmania, and one in Western Australia, the latter being the type locality. Only parthenogenetic females were present in these collections. Their description is incomplete and partially inaccurate. For example, the authors state that there are no head pores, that there is no spine arising from the basal segment of the antennal exopodite, and that the minimum length of females containing eggs is only 0.38 mm, compared with a minimum length of instar-I females of 0.33 mm. These length measurements suggest that the authors might well have had two different but similar appearing species present in their samples. These awkward discrepancies are corrected in the description in this paper.

### Justification for the Genus *Archepleuroxus*

Many of the morphological features of this taxon are shared by the species of *Pleuroxus* and related genera occurring in Australia: 1) the great height of the body of mature parthenogenetic and ephippial females; 2) the presence of a number of short, irregularly curved striae at the anterior end of the shell, and of suggestions of a vague pattern of reticulation posteriorly along the ventral margin; 3) the head pores quite close together and located some considerable distance (about five IP lengths) from the posterior margin; 4) the presence of eight long, two-jointed setae on the antenna; 5) a backward projecting, rounded basal expansion of the antennule; 6) the typically expanded labrum, prolonged into a rather narrow ventral tip; 7) the first trunklimb having the middle seta of the middle group by far the longest; 8) trunklimb II with scraping spines 1 to 3 subequal in length and considerably shorter than spine 4, all provided with many small setules along distal segment; 9) trunklimbs II to V having 8, 8, 6 and 4 gnathobasic filter setae, respectively, and 0, 7, 7 and 4 soft setae, respectively, on the exopodite; 10) ventral setae on shell are all marginal, except for the roughly ten most anterior setae, those in anterior region arising from triangular expansions at base, like teeth; 11) all three male instars being considerably lower in height than females; and 12) the ventral edge of the shell of the mature male anterior to the ventral bulge sloping upward strongly in a straight line and turned inward, thereby obscuring the marginal setae.

The chief differences from the other *Pleuroxus*-like species are in having more than two eggs in the larger parthenogenetic females and two resting eggs in ephippial females, and in the structure of the postabdomen. The latter is shorter and much broader than in any of the other species, it has the marginal denticles nearly all arranged as members of transverse or oblique rows of setae, and it has a complicated pattern of spinular crescents on the lateral surface and particularly along the anal groove and in the preanal region, where there are four chevron-like transverse folds, each with a row of strong setae. The postabdominal claws of male instars II and III are shorter than in the female and are quite distinctly sigmoid, or at least irregularly curved.

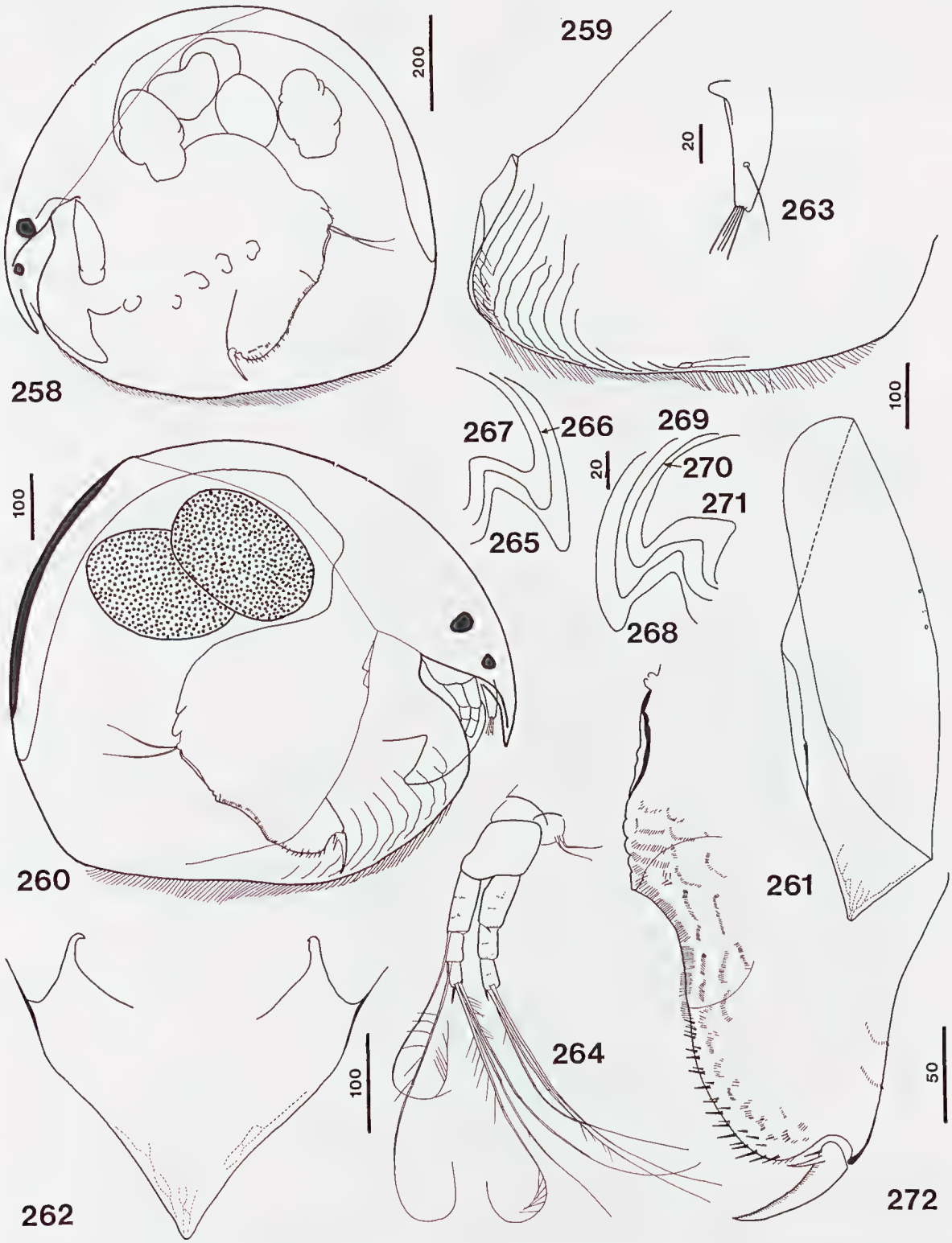
**Material examined.** 128 specimens recovered from Morton's sample 35 from a shallow temporary pond, 21 km north-west of Oatlands, Tasmania, collected 22 Aug. 1974. There was 6 mm of ice on the pond at this time. Smirnov and Timms had 30 samples from this expedition of Morton, which lasted 17 to 27 Aug. 1974, and although they mentioned *Archepleuroxus* being found under ice in a pool near Oatlands, the particular sample I have is not in their overall list nor in their list of positive localities. The sample examined had good numbers of all three instars of males and a few ephippial females, all of which have enabled a complete description of this taxon. Smirnov and Timms had no males.

**Disposition of specimens.** One slide each of a parthenogenetic female, an ephippial female, an instar-I male, an instar-II male, and a mature male, all mounted individually in glycerine jelly, have been deposited in the following museums.

| | AM | NMNZ | BM(NH) | USNMNH |
|---|---|---|---|---|
| parthenogenetic female | P39473 | Cr. 6429 | 1989.616 | 242121 |
| ephippial female | P39474 | – | – | – |
| instar-I male | P39477 | Cr. 6430 | 1989.619 | 242121 |
| instar-II male | P39476 | Cr. 6431 | 1989.618 | – |
| mature male | P39475 | Cr. 6432 | 1989.617 | 242121 |

All the remaining specimens are in the Frey collection in Bloomington.

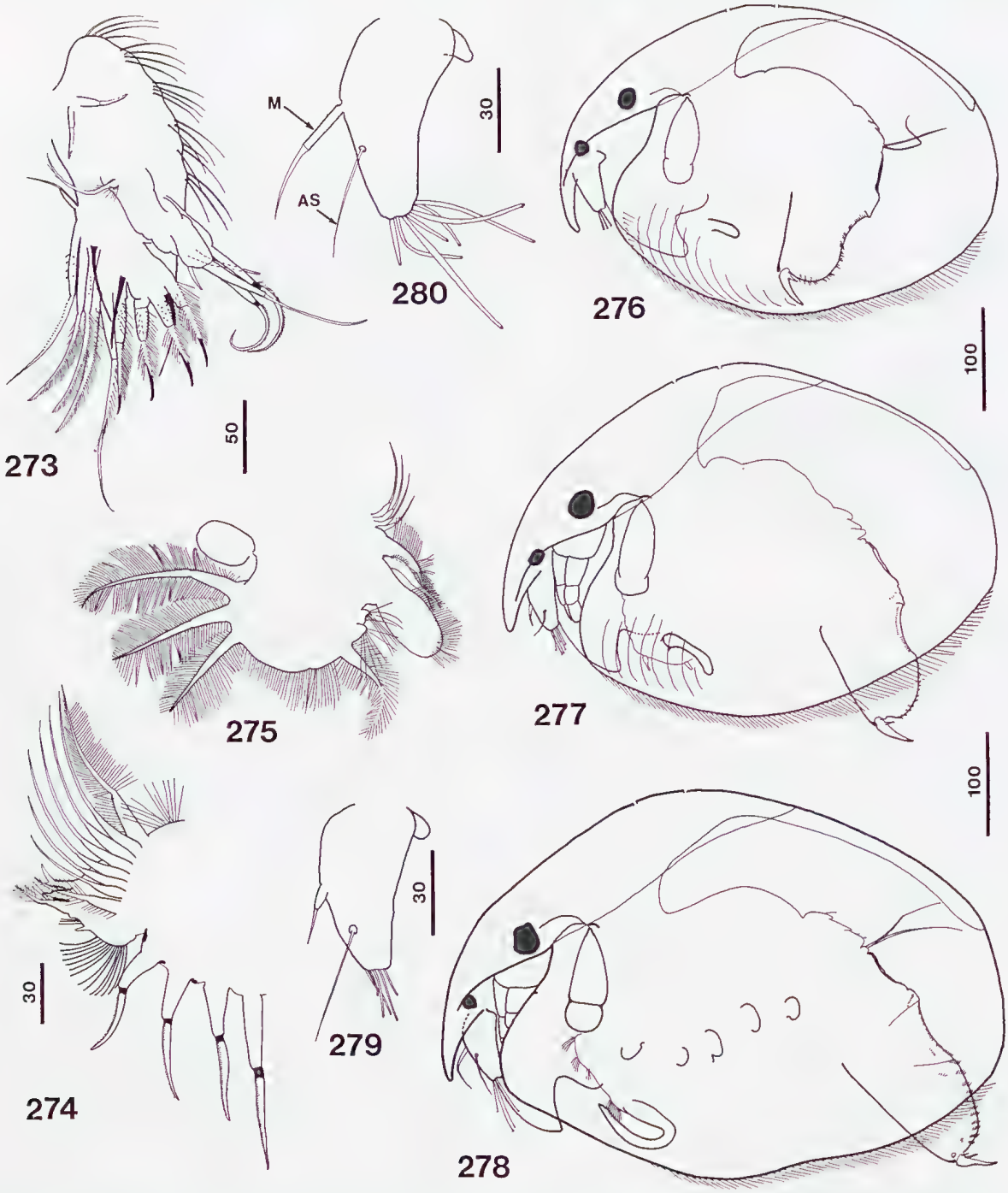
**Parthenogenetic female.** *Shape and shell* (Figs 258, 263, 281, 294, 296). Large females almost as high as long, smaller females relatively more elongate. Dorsal margin highly convex and evenly curved from tip of rostrum to posterior-ventral angle; both posterior-dorsal




**Figs 258-272.** *Archepleuroxus baylyi* Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 258. parthenogenetic female (note the polyembryony); 259. shell of parthenogenetic female; 260. ephippial female, showing the two-egged condition; 261. headshield of parthenogenetic female; 262. rostrum of parthenogenetic female; 263. antennule of parthenogenetic female; 264. antenna of parthenogenetic female; 265-271. labra of parthenogenetic females; 272. postabdomen of parthenogenetic female.

and posterior-ventral angles broadly rounded, with little change in curvature; ventral margin only weakly convex; usually no tooth on shell, but occasionally a very small tooth on one valve, and one specimen had four such teeth on one valve (Fig.296). Moderately flattened from side to side (Fig.294). No keel on head behind pores nor on shell. About 12 curved striae anteriorly on shell, becoming progressively shorter posteriorly (Fig.263). Row of fine marginal setae posterior to last ventral seta or tooth, continuing submarginally toward posterior-dorsal angle (Fig.296). Approximately 91 setae along ventral margin of shell, including about 10 arising from near anterior end projecting inward. Large females polyembryonic (Fig.258), with 22 embryos in holotype.

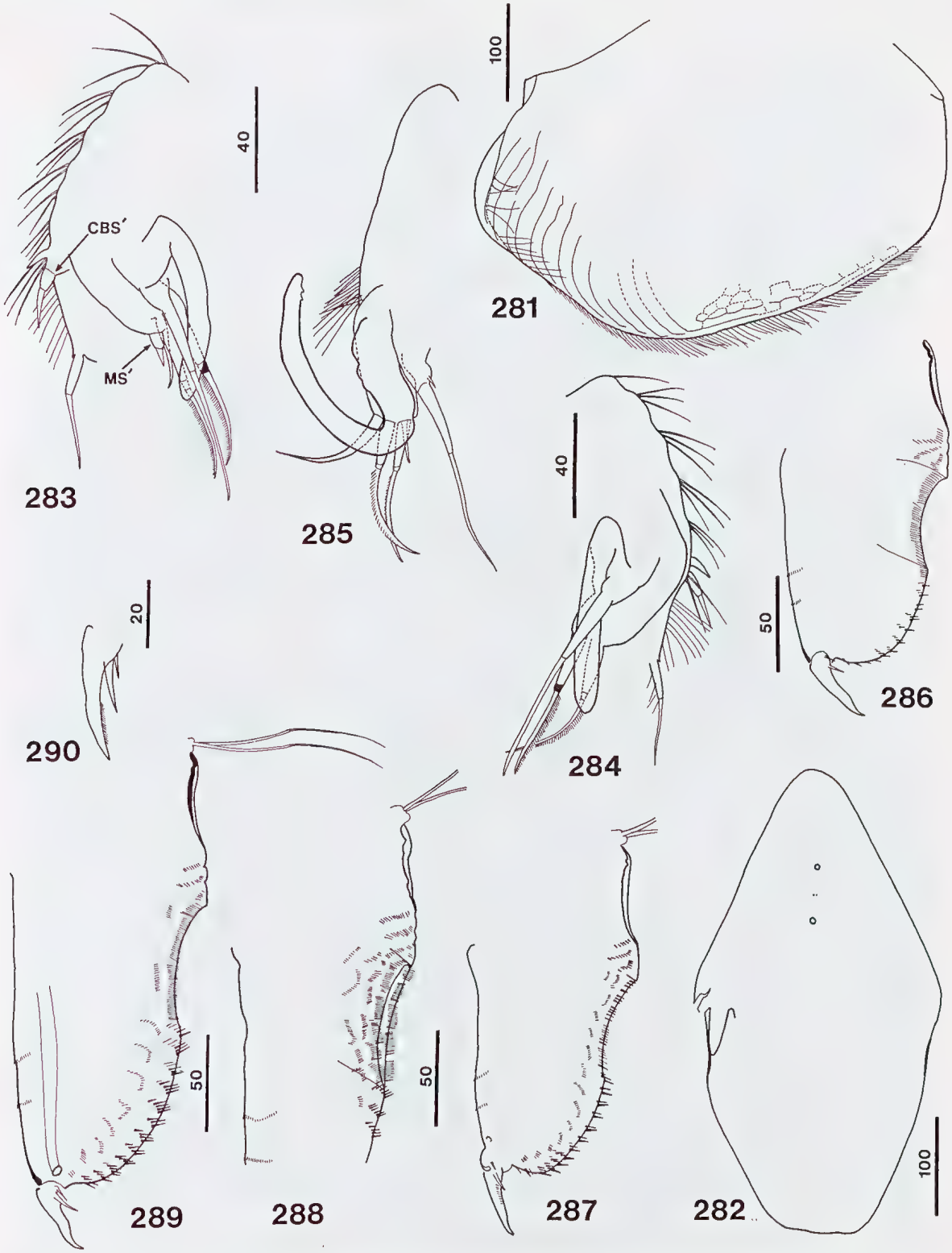
*Head* (Figs 261, 262, 294, 299). Headshield broad, unkeeled (Fig.261). Median pores in adult female about 62 µm apart, located about 4.7 IP distances from posterior end. Rostrum relatively short, bluntly pointed at tip (Figs 262, 299); anterior part with a few indistinct




**Figs 273-280.** *Archepleuroxus baylyi* Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 273. trunklimb I of parthenogenetic female; 274. gnathobase and proximal four scraping spines of trunklimb II, parthenogenetic female; 275. trunklimb V of parthenogenetic female; 276. instar-I male; 277. instar-II male; 278. mature male; 279. antennule of instar-II male; 280. antennule of mature male (note much larger size of aesthetascs than for instar-II antennule; M, male seta; AS, antennular seta).

lines paralleling margin and also a few indistinct meshes. Articulation points for mandibles far removed from headshield-shell junction, as in all species in this paper. Aesthetasc field surrounded by obscure pyramidal tubercles.

*Antennule* (Figs 263, 282, 295). Elongate, slender, evenly curved. Nine aesthetascs, about one third to two fifths length of antennule. Antennular seta arising about one third from distal end, longer than aesthetascs. Rounded protuberance at base, projecting posteriorly. Aesthetascs unequal in length, tips do not reach tip of rostrum.

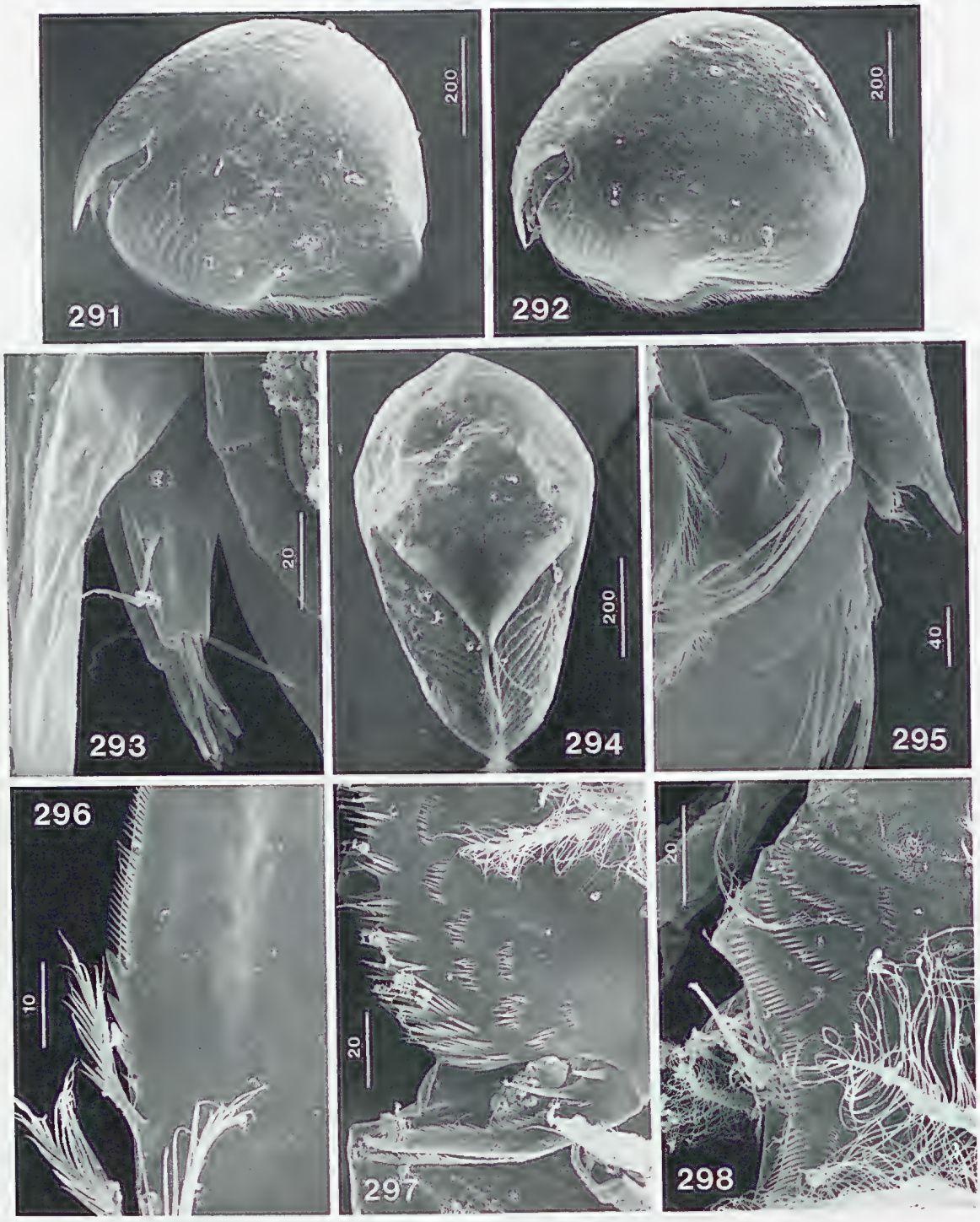



**Figs 281-290.** *Archepleuroxus baylyi* Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 281. shell of mature male; 282. headshield of mature male; 283, 284. part of trunklimb I of instar-II male (CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 285. part of trunklimb I of mature male; 286, 287. postabdomen of instar-II male; 288, 289. postabdomen of mature male (note irregular claw); 290. postabdominal claw of mature male.

*Antenna* (Figs 264, 295). Formula: 0(1)-0-3(1)/1-1-3(1). Setae from basal and middle segments of endopodite both very long. Three long terminal setae on each branch, one somewhat shorter than other 2. Terminal spines short, less than half length of segment to which attached. Very small spine from basal segment of exopodite.

*Labrum* (Figs 265-271, 295, 314). Large, elongate; anterior margin convex, usually smoothly but sometimes irregularly; tip narrowly rounded; posterior margin concave, usually with distinct angle one third to one half from tip; posterior angle narrow and less than 90°.

*Trunklimb I* (Fig.273). Two setae on ODL, smaller one with no distal spinules, only one about one third length of basal segment of longer seta; 3 IDL setae, 2




**Figs 291-298.** *Archepleuroxus baylyi* Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 291. parthenogenetic female; 292. ephippial female; 293. antennule of parthenogenetic female; 294. frontal view of parthenogenetic female; 295. labrum, antennules, and antenna of parthenogenetic female; 296. posterior-ventral angle and adjacent area of posterior margin of shell of parthenogenetic female (only specimen observed with more than one tooth at the angle); 297, 298. postabdomen of parthenogenetic female.

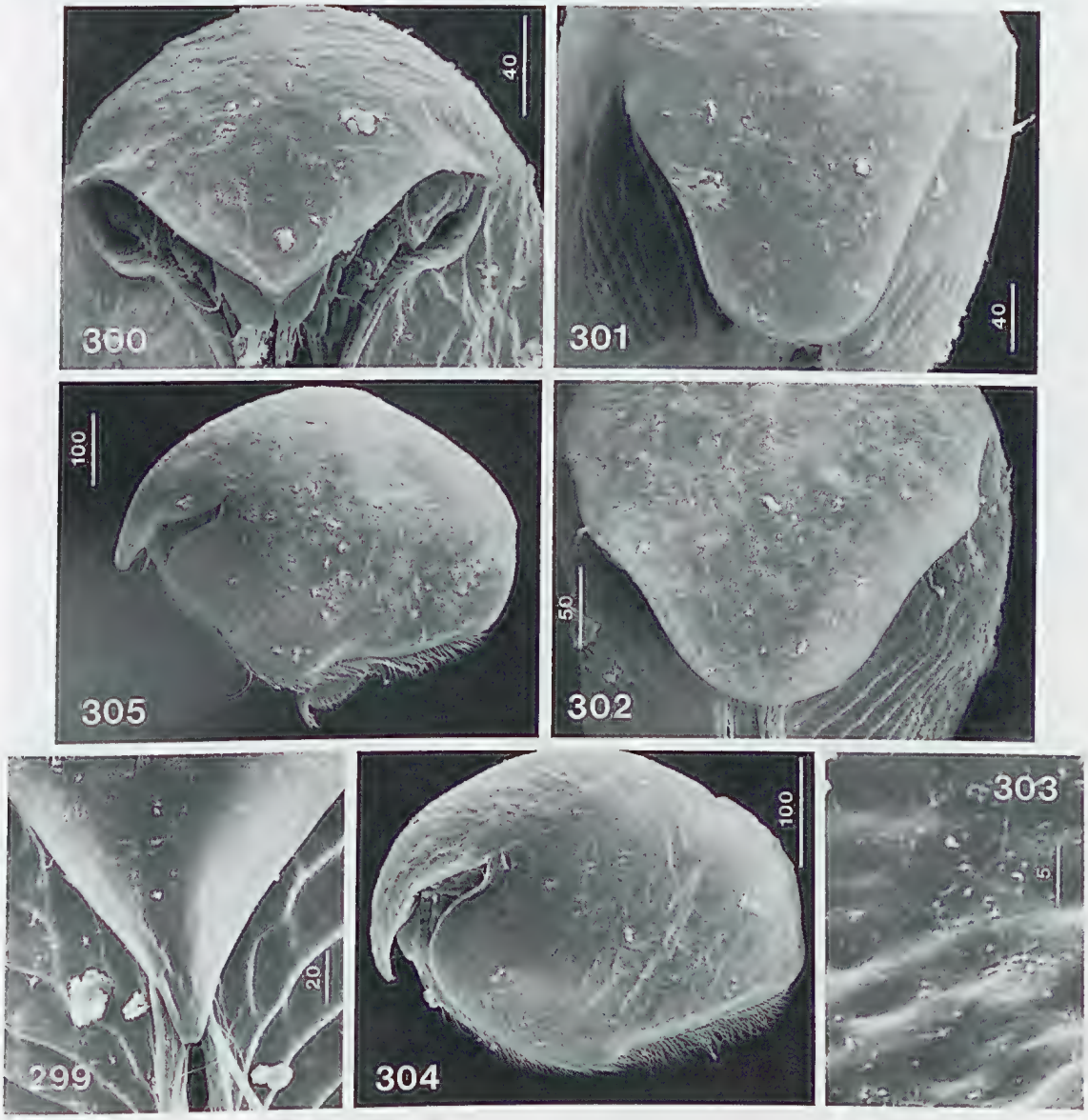
long with setose distal segment, other only about as long as proximal segments of longer setae, seems unarmed under phase optics. Lateral seta well developed. Middle seta of middle group of corm setae longest. All 3 accessory setae long, well developed.

*Trunklimb II* (Fig.274). Scraping spines 1-3 subequal in length, considerably shorter than spine 4, all with very fine and almost uncountable spinules along margin of distal segment. Three gnathobasic setae and one much smaller and blunter seta on margin toward scraping spines, the latter preceded by 3 straight setae and followed by about 15 stout curved setae, of which the first several have setules near their tips. Eight gnathobasic filter setae.

*Trunklimbs III-V*. Only limb V (Fig.275) clear in dissection. Exopodite soft setae numbered 7, 7 and 4, and the gnathobasic filter setae 8, 6 and 4, respectively.

*Postabdomen* (Figs 272, 297, 298). Relatively short, broad. Anal groove shorter than preanal and postanal parts, which are subequal. Preanal portion with series of 3-4 scallops near preanal angle, representing rounded ridges across margin and angled distally on either side, like chevrons. Postanal portion with about 12 positions for denticles, each position except a few of most distal ones occupied by short row of denticles or setae arranged transverse to margin. Lateral surface with irregular row of scallops of setae, with 3-4 rows along anal groove and in preanal region. Two scallops of short setae across ventral margin. Anal groove bordered by about 5 distinct groupings of setae arranged sequentially. Abdominal setae short, barely reaching anal groove when extended.

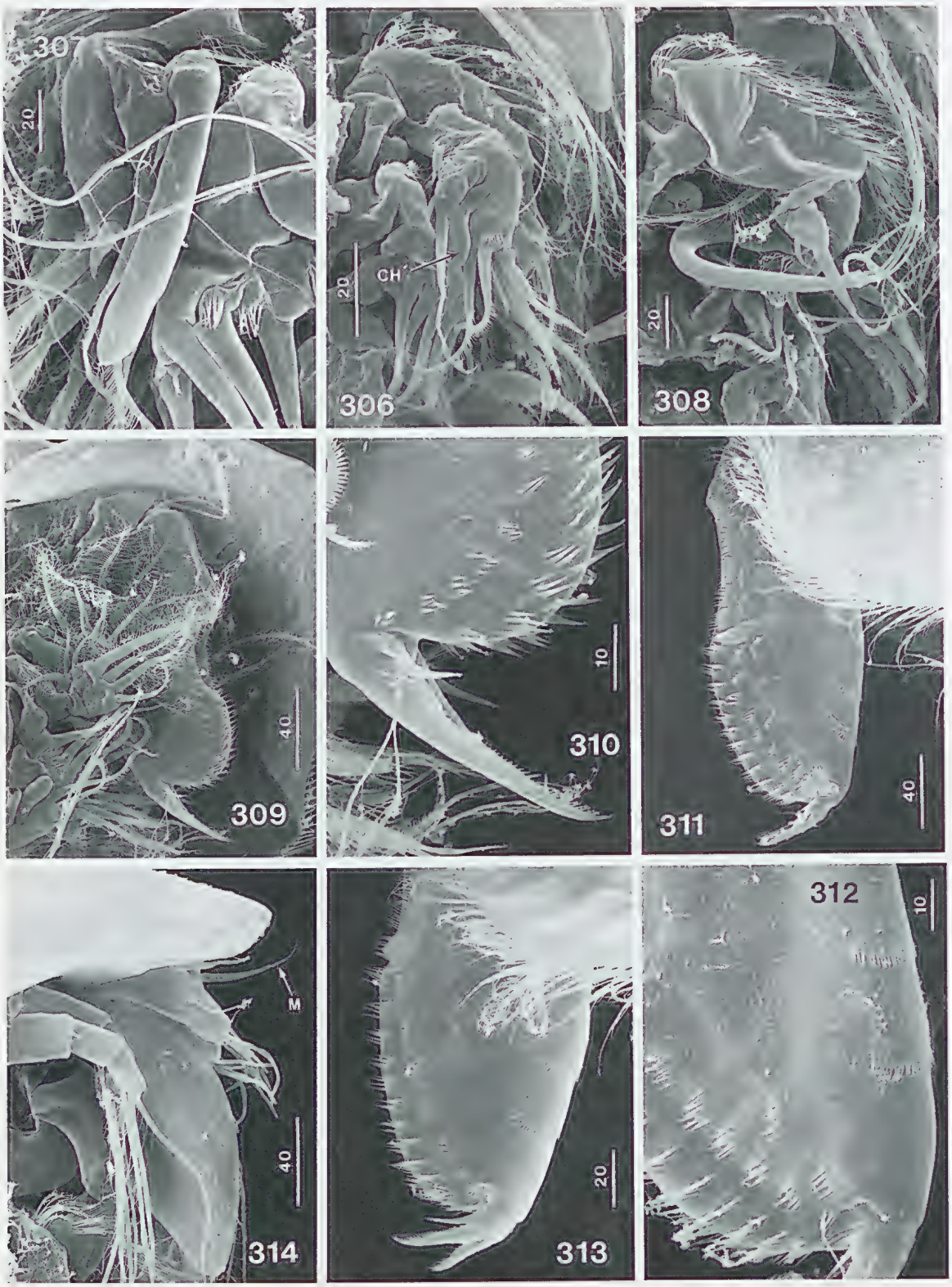
*Postabdominal claw* (Figs 272, 297). Stout, evenly curved, with fine setules along entire concave margin. Two basal spines, longer one slender, curved, about as long as basal width of claw; shorter one very slender,




**Figs 299-305.** *Archepleuroxus baylyi* Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 299. Rostrum of parthenogenetic female; 300. rostrum of instar-I male; 301. rostrum of instar-II male; 302. rostrum of mature male; 303. surface patterning of shell of ephippial female; 304. instar-I male; 305. mature male.

straight, only about half as long.

**Ephippial female** (Figs 260, 292, 303). Two ephippial eggs. Ephippial portion of shell heavily pigmented. Headshield narrower posteriorly than in parthenogenetic female to meet contracted shell, with which it forms a distinct angle in outline (Fig.260); distinct triangular expansion at beginning of slough line. Dorsal edge thickly chitinised. Surface of ephippium finely dimpled (Fig.303), but no other sculpturing.




**Figs 306-314.** *Archepleuroxus baylyi* Smirnov & Timms, 1983. All specimens from Morton sample 35 (pond near Oatlands, Tas., 22 Aug. 1974). 306. trunklimb I of instar-I male (CH', anlage of copulatory hook); 307. trunklimb I of instar-II male; 308. trunklimb I of mature male; 309, 310. postabdomen of instar-I male; 311-313. postabdomen of mature male; 314. rostrum, antennules, antenna, and labrum of mature male (M, male seta).

Other details of morphology same as in parthenogenetic female.

**Male.** Copulatory hook develops gradually (Figs 276-278, 283-285, 306-309). Anlagen of copulatory brush seta (actually 2 anlagen here), of male IDL seta on trunklimb I (Figs 283, 284), and of male seta on antennule (Figs 277, 239) appear in instar-II. Rostrum shorter than in female, pointed in instar-I (Fig.300); rounded and progressively shorter in instars II and III (Figs 282, 301, 302), first with only the aesthetascs and then antennule also projecting beyond tip of rostrum. Postabdomen similar in shape and armament to that of female, although less broad (Figs 286-289, 309-313); genital pore moves progressively distad to its definitive position in instar-III slightly lateral near base of postabdominal claw (Figs 289, 312). Postabdominal claw of instars II and III shorter than in female and somewhat sigmoid (Figs 286, 287, 311, 313). In shape, all three instars more elongate (less high) than corresponding instars of females (Figs 276-278, 304, 305). PP distance only twice IP distance (or even a little less in instar-I), contrasting with 4.7 times IP distance in mature parthenogenetic and ephippial females. Postabdomen of all 3 instars provided throughout postanal region with transverse groups of stoutly chitinised setae (Figs 286, 287, 289, 309-313). Mature male seems to have only 9 aesthetascs, and certainly fewer than 12, some of which are about two thirds length of antennule, and all much longer and thicker than in instar-II male (compare Figs 279 and 280) or in females.

**Length.** Females: 0.39-0.95 mm (n=128); instar-I 0.39-0.44 mm (n=14); instar-II 0.49-0.56 mm (n=31); smallest parthenogenetic female with eggs 0.62 (n=27); ephippial females 0.67-0.78 mm (n=3). Males: instar-I 0.39-0.43 mm (n=14); instar-II 0.44-0.50 mm (n=9); instar-III (= mature) 0.51-0.56 mm (n=17).

## *Plurispina* n.gen.

**Type species.** *Plurispina chauliodus* n.sp. by original designation.

**Diagnosis.** The following characters are shared by the two species described here: 1) a comparatively large number of setae in the gnathobasic filter combs of trunklimbs II-V - 10, 10, 7 and 5, respectively, instead of the more common 8, 8, 6 and 4; 2) shell and head covered by small rounded tubercles, which in the case of *P. multituberculata* are so densely placed that they create a general opacity; 3) radial ridges on shell and raised meshes on dorsal part of shell and adjacent headshield; 4) a strong keel beginning immediately behind posterior headpore, continuing to posterior-dorsal angle of shell, and 5) a strong flaring out proximally of the ventral margin of the postabdomen. Parthenogenetic females of both taxa are high in relation to length, with dorsal margin highly arched and ventral margin much less so. The posterior-dorsal corner of the shell is essentially absent as any perceptible change in curvature here, and the posterior-ventral angle is likewise almost eliminated. Here in both species there is a very small rounded or triangular tooth, with number per valve varying from none to two. Ventral setae, including inwardly directed anterior setae, average 107 in *P. chauliodus* and 122 in *P. multituberculata*; those anterior to the midventral bulge have expanded bases that are strongly chitinised and superficially resemble the teeth of a saw.

**Etymology.** From (L) *plus*, *pluris* more, and (L) *spina* spine (feminine gender), referring to the larger number of setae in the gnathobasic filter combs of trunklimbs II-V.

**Remarks.** Other than number of setae, the morphology of the two species is rather divergent, so that not too much can be said about common characters. Unfortunately, no males of *Plurispina multituberculata* are available, and hence there is no way of knowing if the brush-like nature of the male seta on the antennule in *Plurispina chauliodus*, the general shape and armament of the male postabdomen, and the presence of two prominent submarginal denticles on the rostrum of the male are unique for this species or characteristic of the genus.

### *Plurispina chauliodus* n.sp.

Figs 315-375

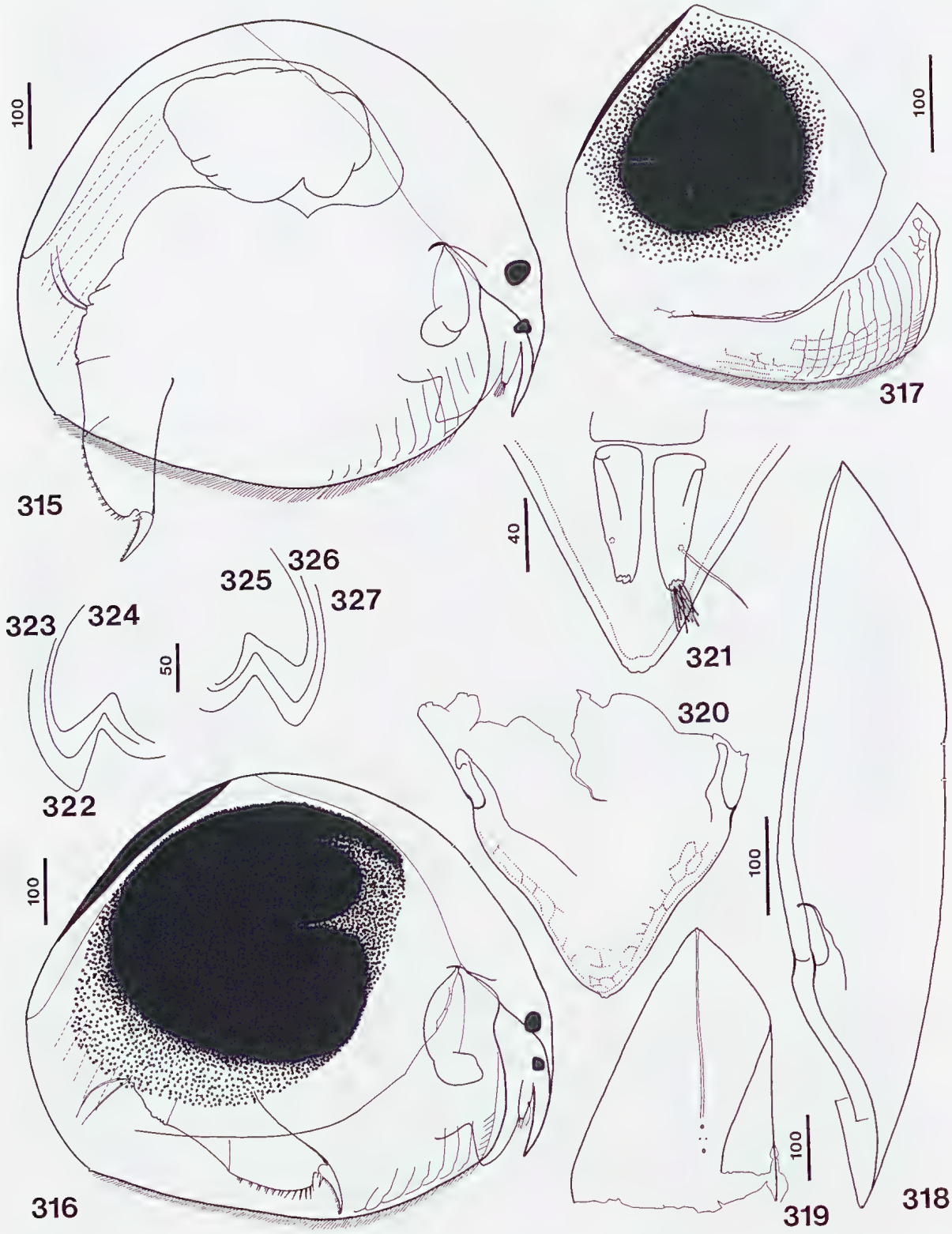
*Pleuroxus jugosus*.–Smirnov & Timms, 1983: 22-24, figs 21, 22 (not *Chydorus jugosus* Henry, 1922).

**Etymology.** From (Gr) *chauliodus* with projecting teeth, or tusked (common gender), referring to two prominent submarginal denticles on rostrum of mature male.

**Remarks.** Smirnov & Timms (1983) used specimens from Bayly's sample 58 (their sample 420) to expand the morphological understanding of Henry's taxon. They included drawings of a female and its headshield, postabdomen and head pores, and of a mature male with its postabdomen and tip of the rostrum. They pointed out that the shell and head are finely punctate (= tuberculate) and that the rostrum of the male is provided with two spines, the latter being a character "...not described for any other cladoceran..." Unfortunately, all these new morphological details do not apply to *Pleuroxus jugosus* at all, as the two taxa are even in different genera. The description of *P. jugosus*, incomplete though it is without mature females, males, and ephippial females, will be as given later in this paper.

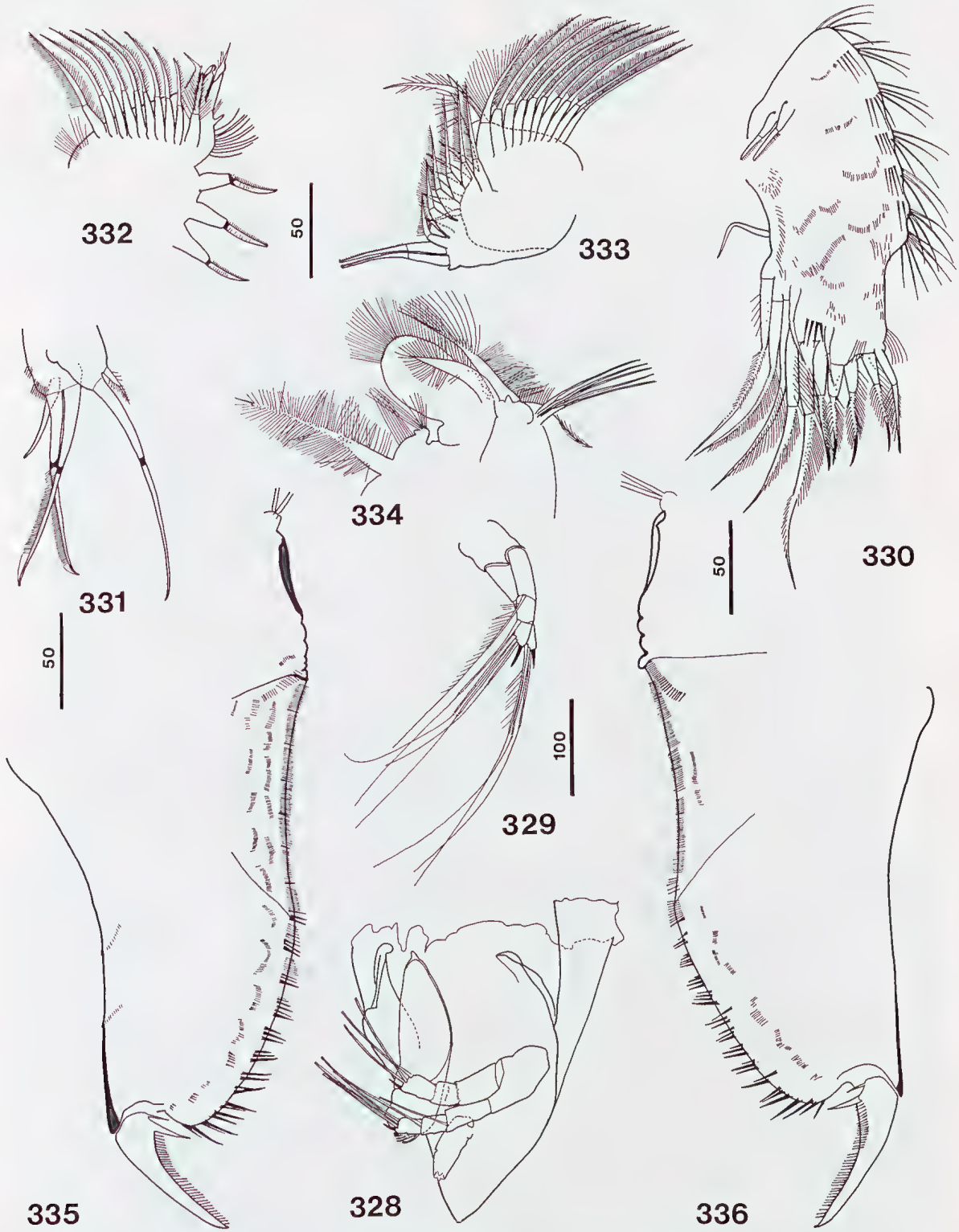
**Material examined.** *Type locality.* Granite pool in Muirillup Rock near Northcliffe, WA (Bayly, 1982: fig.4), collected by I.A.E. Bayly: sample 31 on 4 June, sample 58 on 18 June (= Smirnov & Timms sample 420), and sample 84 on 2 July, all in 1977. Numbered N11 in Bayly's system, this pool measured 2.8 x 1.4 m and was 4 cm deep. Its pH varied from 5.8 to 6.4, and its conductivity at 18°C was 61-70 µS $cm^{-1}$.

**Types.** 167 specimens from samples 31 (83 individuals), 58 (49), and 84 (25), plus various exoskeletal components. Specimens from the three




**Figs 315-327.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly samples 31, 58, and 84 (granite pool on Muirillup Rock near Northcliffe, WA, 4 and 18 June and 2 July 1977, respectively). 318 and 319 are from sample 31; 315 and 321-327 are from sample 58; and 316, 317, and 320 are from sample 84. 315. parthenogenetic female; 316. ephippial female; 317. ephippium; 318-321. headshield of parthenogenetic females with antennules included in 321; 322-327. labra of parthenogenetic females.

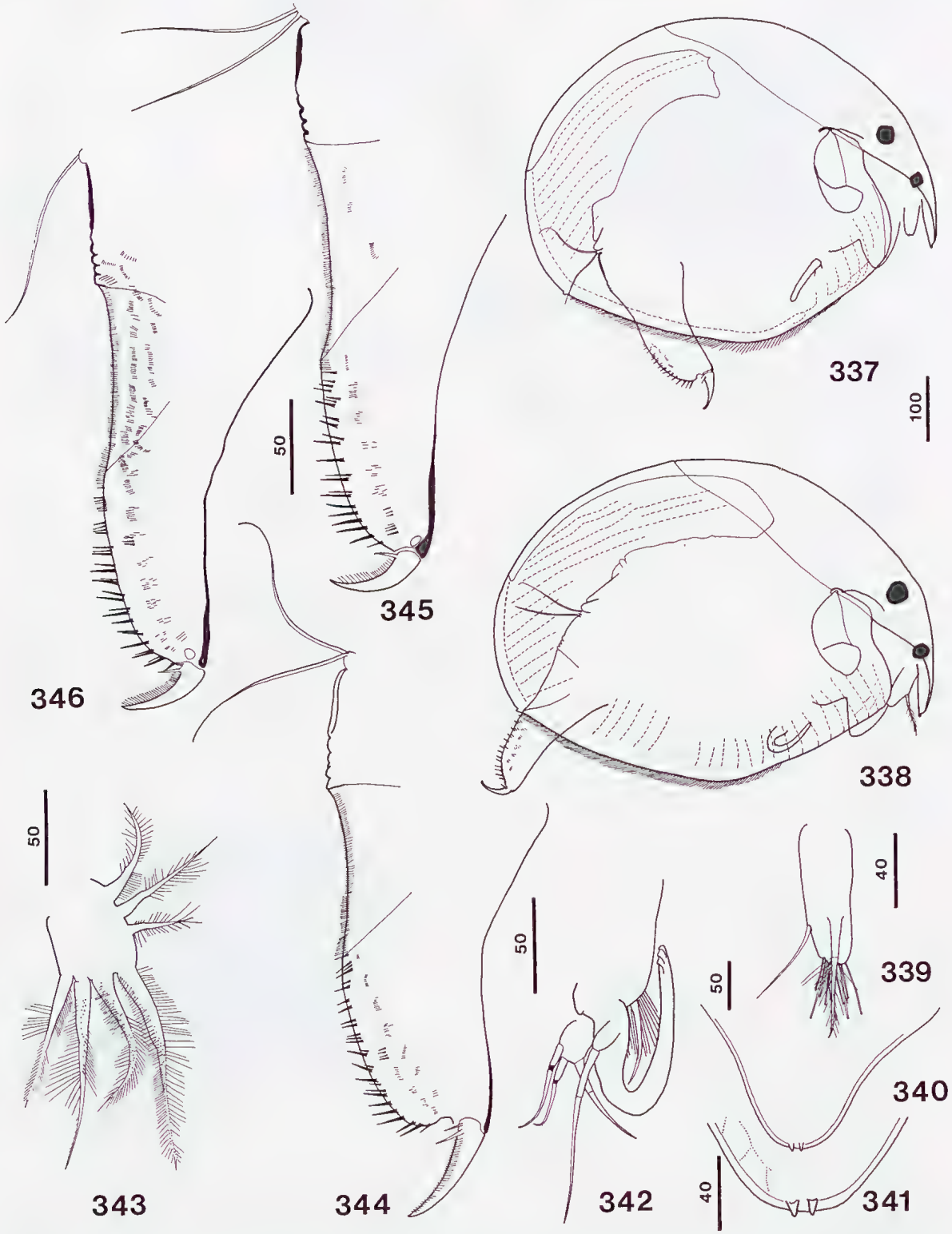
samples agree exactly in their morphology and size relationships. Drawings from all three are included in the description. Registration numbers are given in parentheses below. HOLOTYPE – a mature parthenogenetic female 0.70 mm long, mounted on a slide in glycerine jelly, AM (P39478). ALLOTYPE – a mature male 0.62 mm long, mounted on a slide in glycerine jelly, AM (P39479). Special PARATYPE – an




**Figs 328-336.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly samples 31, 58, and 84 (granite pool on Muirillup Rock near Northcliffe, WA, 4 and 18 June and 2 July 1977, respectively). 328 is from sample 31, 329 from sample 84, and all others are from sample 58. 328. rostrum and associated head appendages of parthenogenetic female; 329. antenna of mature male; 330, 331. trunklimb I of parthenogenetic female (330 is a medial view without the ODL and IDL; 331 is only of the ODL and IDL; ODL2, shorter ODL seta, feathered); 332. gnathobase and three adjacent scraping spines of trunklimb II of parthenogenetic female; 333.gnathobase of trunklimb III of parthenogenetic female; 334. gnathobase of trunklimb V of parthenogenetic female; 335, 336. postabdomen of parthenogenetic female.

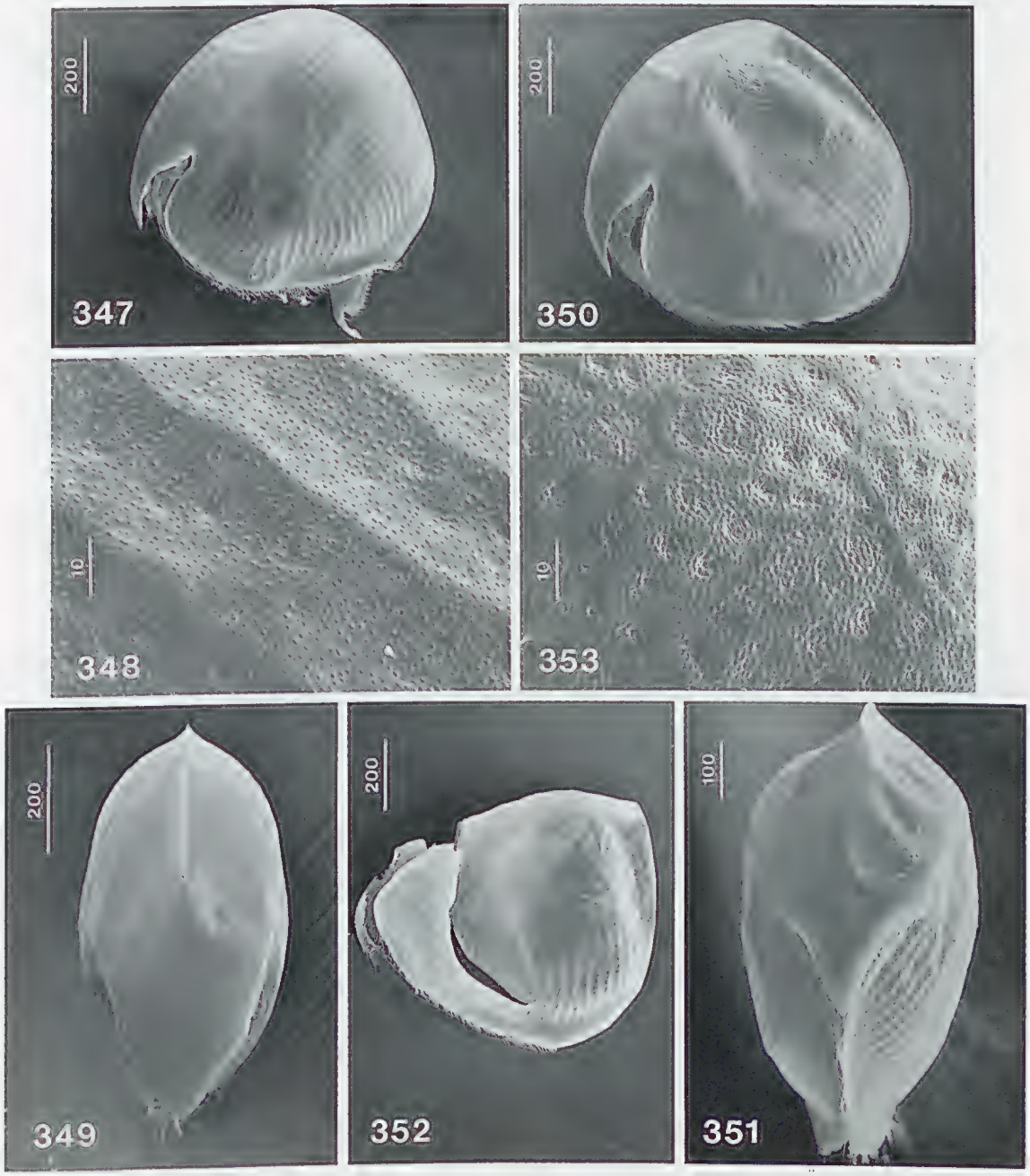
ephippial female 0.89 mm long, mounted on a slide in glycerine jelly, AM (P39480). PARATYPES – 1 slide each in glycerine jelly of a mature parthenogenetic female, a mature male, and an ephippial female have been deposited in each of the following museums.

| | NMNZ | BM(NH) | USNMNH |
|---|---|---|---|
| parthenogenetic female | Cr. 6433 | 1989.620 | 242122 |
| mature male | Cr. 6434 | 1989.621 | 242122 |
| ephippial female | Cr. 6435 | 1989.622 | 242122 |




**Figs 337-346.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly samples 58 and 84 (granite pool on Muirillup Rock near Northcliffe, WA, 18 June and 2 July 1977, respectively). 337 and 344 are from sample 58, the rest from sample 84. 337. instar-II male; 388. mature male; 339, antennule of mature male; 340, 341. tip of labrum of mature male, showing two submarginal tusk-like denticles; 342. ODL and IDL of trunklimb I of mature male; 343. exopodite of trunklimb III of mature male; 344. postabdomen of instar-II male (genital pore not visible); 345, 346. postabdomen of mature male.

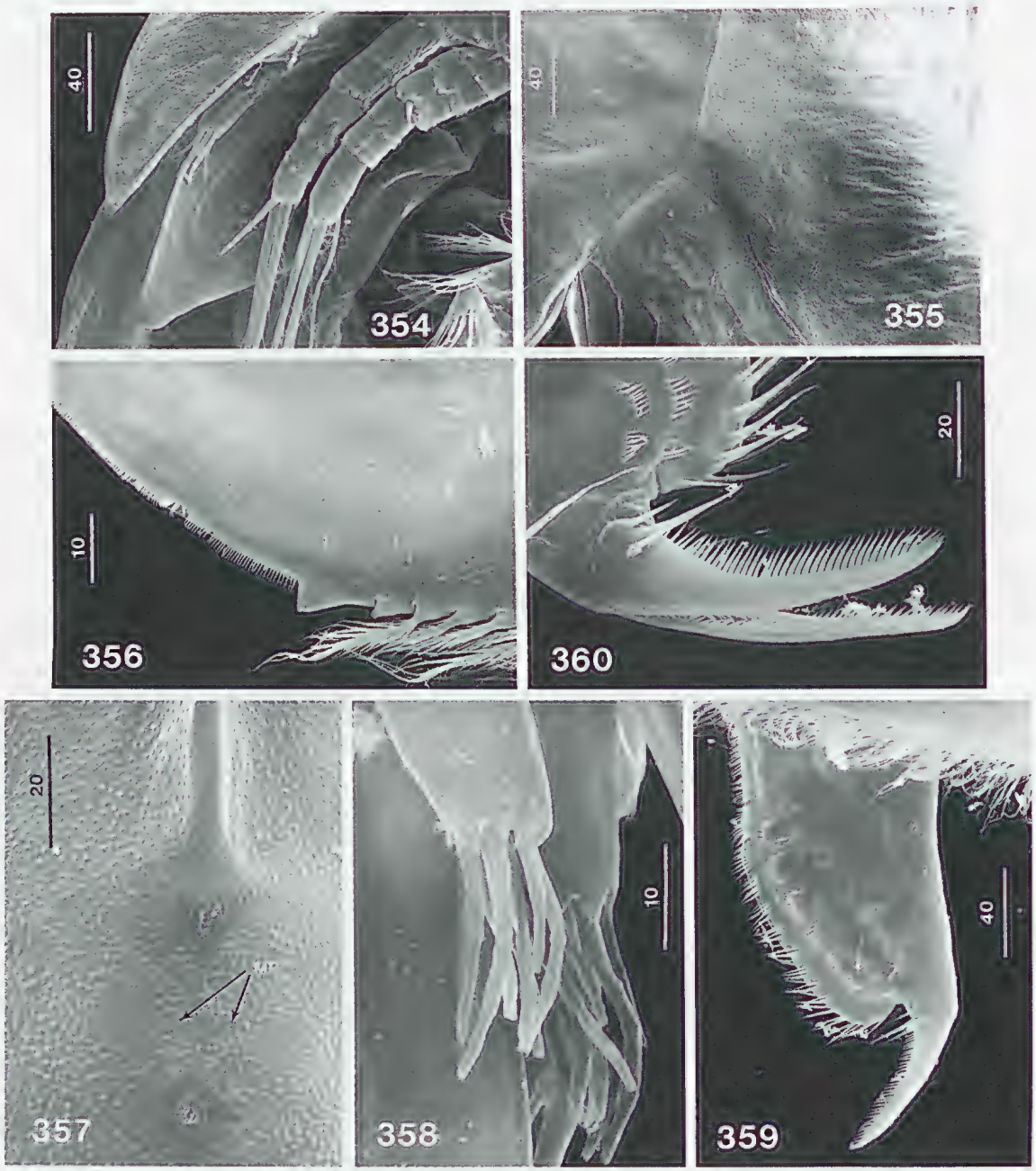
**Diagnosis.** Body almost as high as long, evenly curved dorsally, with posterior-dorsal angle virtually lacking. Shell with series of interrupted curved striae anteriorly, and with straight cross connections formed by rows of tubercles; radiating ridges along ventral and dorsal margins; about 107 ventral setae, ending posteriorly in a small, broad-based triangular tooth, followed by a marginal-submarginal row of short but regular setules extending to posterior-dorsal angle; tip of rostrum weakly bifid. Short seta on ODL well developed and brush-like. Ten, 10, 7 and 5 setae in gnathobasic filter combs of trunklimbs II to V, respectively, and the more typical 7, 7 and 4 feathered exopodite setae on limbs III-V. Postabdomen with preanal portion much shorter than anal or postanal portions, provided distally with 4 or 5 distinct rounded scallops resulting from rounded chevron-like folds across dorsal margin; 12-15 denticles or denticle positions, mostly multiple, and all members long and slender; abdominal setae short, not extending far into anal groove region when depressed. Postabdominal claw with long and strong setae along dorsal margin; basal spines thin and relatively short. Ephippial female with very dark pigmentation that obscures morphological details; single resting egg. Male II with more slender postabdomen than female; genital pore near base of




**Figs 347-353.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 347. parthenogenetic female; 348. fine tubercles on shell of parthenogenetic female; 349. top view of parthenogenetic female, showing shape of headshield and marked keel beginning just behind posterior headpore; 350. ephippial female; 351. front view of ephippial female, showing rostrum and sharp keel beginning just behind posterior headpore; 352. ephippium; 353. surface patterning of dimples and tubercles in ephippial portion of shell.

claw; well developed male seta anlage on antennule. Male III has shortened rounded rostrum with 2 stout submarginal denticles; male seta on antennule long, distal segment brush-like; postabdomen slender, tapered to base of claw, provided with about same number of denticle positions as in female but all denticles stout and well chitinised; postabdominal claw shorter and stouter than in female, strongly curved, provided with long setae along concave margin. Colour dark.

**Parthenogenetic female.** *Shape and shell* (Figs 315, 347-349, 356, 492). Body very high, but still somewhat longer than high; dorsal margin evenly curved from tip of rostrum to posterior-ventral angle, with only small convexities over eye and ocellus (Fig.315); posterior margin short, weakly but evenly convex; ventral margin convex, with maximum curvature (= ventral bulge) just anterior to middle. Shell covered nearly everywhere by radiating ridges, about 7-11 of those in front associated with short striae paralleling anterior margin of shell (Fig.317), those behind associated with rows of tubercles, which also produce cross connections; row



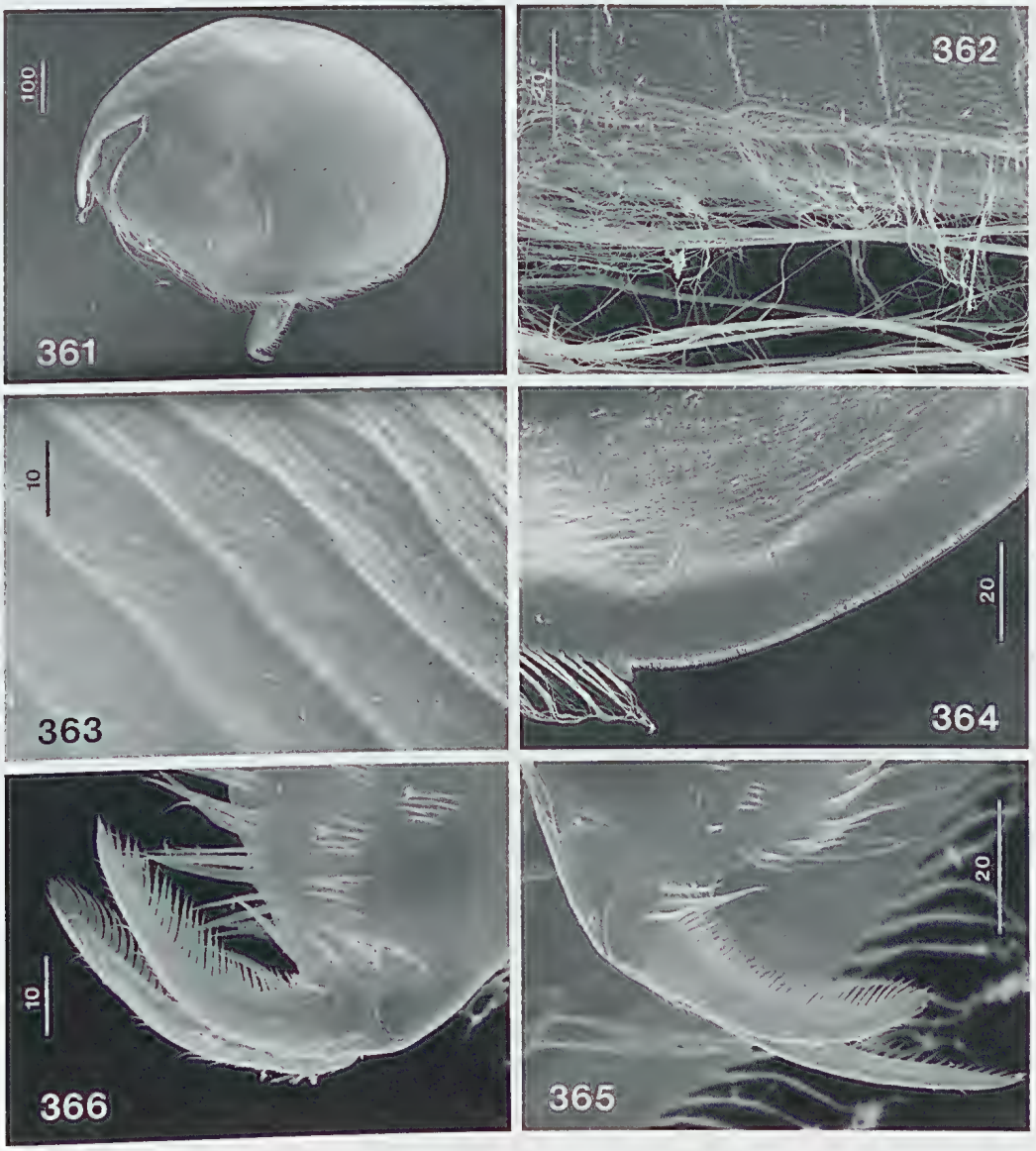

**Figs 354-360.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 354. head end of parthenogenetic female, showing rostrum, labrum, antennule, and antenna (note long terminal spines on antenna); 355. junction of ecdysial line and slough line on shell of ephippial female; 356. posterior-ventral angle with small shell tooth and with adjacent setulated portion of posterior margin, parthenogenetic female; 357. headpores and keel of parthenogenetic female (MP, minor pores); 358. antennules of parthenogenetic female, showing pointed triangles surrounding aesthetasc field; 359. postabdomen of parthenogenetic female; 360. postabdominal claw of parthenogenetic female (note straight basal spines and long setae along concave margin).

of 107 setae (range 100-113, n=17) along ventral edge of shell, including those turned inward at anterior end, terminating at a broad-based triangular denticle at posterior-ventral angle, which is followed by a marginal-submarginal row of closely spaced setae that continue toward posterior-dorsal angle (Fig.356). Entire surface of shell and head, except for marginal borders, covered with rather densely spaced, rounded tubercles (Figs 348, 357). Strong keel on head beginning immediately behind posterior pore (Figs 349, 357), continuing to posterior-dorsal angle. Colour dark brownish, and hence difficult to discern details.

*Head* (Figs 318-321, 328, 349, 357). Rostrum short and broad (Fig.320), weakly bifid at tip (Fig.321); suggestions of submarginal line and meshes from the lining up of denticles into rows. IP distance roughly 42 µm; PP distance 7.6 times IP distance or even more; strong keel behind posterior pore, sometimes produces change in curvature as seen from side. Minor pores about two major pore diameters apart (Fig.357).

*Antennule* (Figs 321, 358). Long and narrow, tapering toward distal end, which is provided with series of triangular tubercles around aesthetasc field; rounded evagination directed posteriorly at base; 9 aesthetascs, all terminal, about one third length of antennule; antennular seta about twice as long, arising about one third from tip of antennule; tips of aesthetascs much shorter than tip of rostrum.

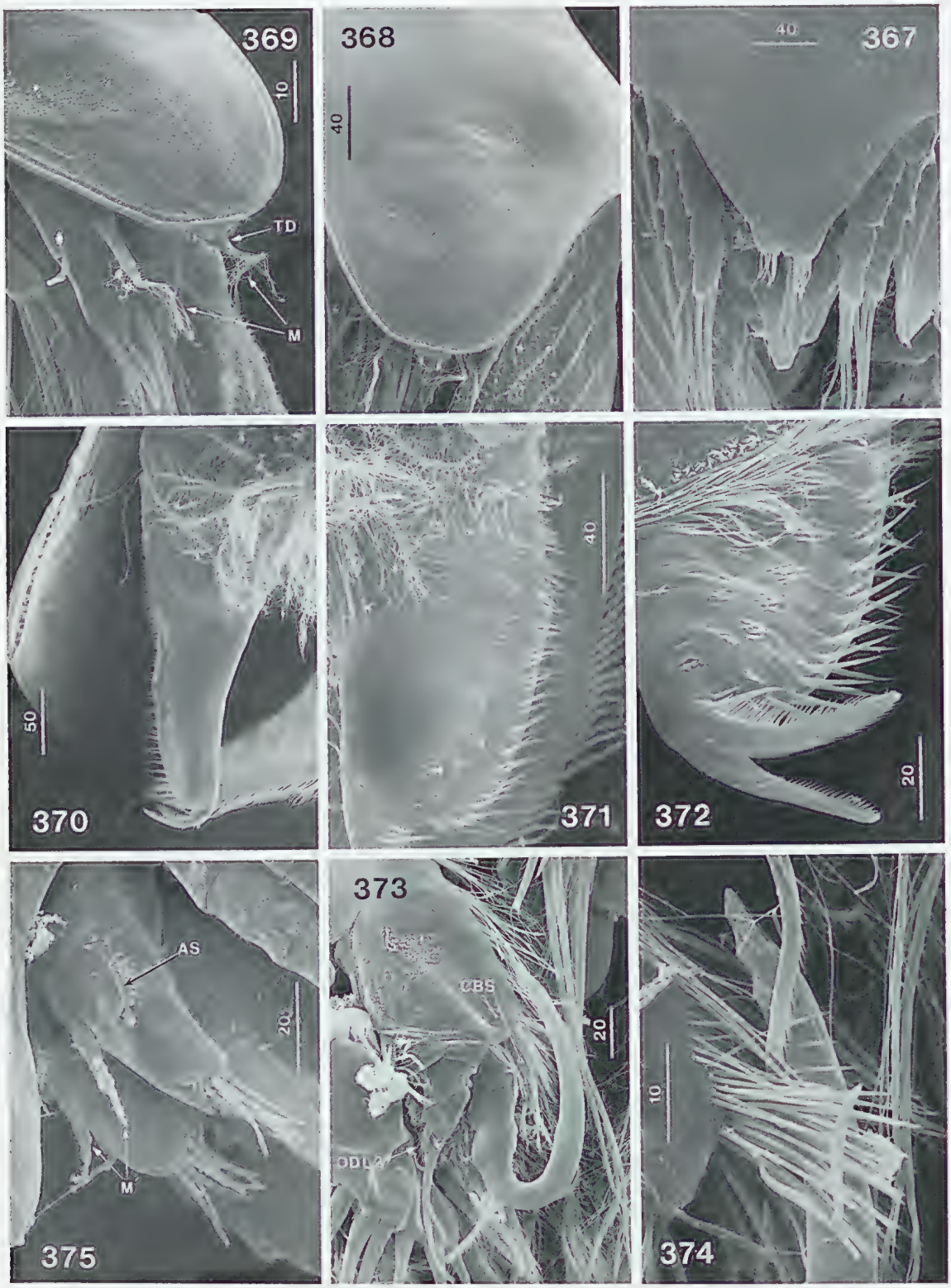
*Antenna* (Figs 328, 329, 354, 367). Formula: 0(1)-0-3(1)/1-1-3(1). Eight long swimming setae; one of 3 terminal setae on endopodite considerably shorter than other 2, about same length as long seta arising from basal segment of endopodite. Both terminal spines long, about as long as segments from which they arise, and spine




**Figs 361-366.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 361. mature male; 362. anterior margin of shell of mature male, showing dense mass of long fine setae occurring here; 363. surface of shell of mature male, showing radiating ridges and fine tubercles; 364. inside view of posterior-ventral angle and posterior margin of shell of mature male; 365. postabdominal claws of instar-II male; 366. postabdominal claws of mature male.

from basal segment of exopodite well developed. Transverse rows and crescents of fine spinules on 3 segments of both rami and on basal segment.

*Labrum* (Figs 322-327, 354). Broad, and with rather short tip, which is usually quite broadly rounded; anterior margin evenly curved; posterior margin mostly straight, sometimes weakly convex; posterior angle often quite narrow, less than 90°.




**Figs 367-375.** *Plurispina chauliodus* n.sp. All specimens PARATYPES from Bayly sample 84 (granite pool on Muirillup Rock near Northcliffe, WA, 2 July 1977). 367. rostrum of instar-II male; 368-369. rostrum of mature male, showing the two submarginal tusk-like denticles (TD) and the highly feathered male seta on the antennule (M); 370-372. postabdomen and claws of mature male; 373. trunklimb I of mature male, showing slender copulatory hook (ODL2, short seta on ODL, feathered; CBS, copulatory brush seta); 374. attenuated tip of copulatory hook of mature male; 375. antennules of instar-II male (M', anlage of male seta; AS, antennular seta).

*Trunklimb I* (Figs 330, 331). Small seta on ODL, almost half as long as basal segment of longer ODL seta; with distal segment brush-like from short setules; 3 setae on IDL, shortest of which barely reaches tip of basal segment of other 2. Middle seta of middle group of corm setae the longest.

*Trunklimb II* (Fig.332). Ten setae in gnathobasic filter comb; 3 gnathobasic setae, followed toward scraping spines by 3 straight slender setae, then a well-developed thickened seta or denticle, and this by about 10 long, thick setae curving distally toward gnathobase. Scraping spines 7 and 8 considerably longer than expected from mere increase in size sequentially; other 6 scraping spines with very fine setules along outer segment.

*Trunklimbs III-V* (Figs 333, 334, 343). Setae in gnathobasic filter comb number 10, 7 and 5 (4 in male), respectively, and 7, 7 and 4 feathered setae on the exopodite, respectively. On trunklimb III, the 2 'hard' setae farthest from gnathobase are heavily chitinised and almost spine-like (Fig.333), projecting ventrally in intact animal in opposition to trunklimb I, especially; longest feathered seta on exopodite only slightly longer than next longest (Fig.343).

*Postabdomen* (Figs 335, 336, 359, 493). Anal groove about as long as postanal portion; preanal portion much shorter, with a series of 4-6 distinct rounded scallops in margin distally. About 12-15 marginal denticle positions; denticles long and slender, seldom single except occasionally distally, organised into a series of clusters or rows proximally, which are oriented parallel to margin. Preanal and postanal angles, especially the latter, very weakly developed; anal groove protected by series of about 7 groups of slender setae projecting beyond margin; distalmost member of each group stouter (Fig.335). Postanal portion with single row of curved crescents laterally, 2 rows along anal groove, and essentially none in preanal region. Two big crescents of fine spines across ventral margin. Abdominal setae short, reaching only to about proximal third of anal groove when extended. Ventral margin flares outward basally.

*Postabdominal claw* (Figs 335, 336, 359, 360). Stout; rather blunt toward tip; concave margin curved about one third from base, then almost straight to tip. Concave margin with 2 series of long and conspicuous spinules, extending to tip, those in distal series longer. Two short basal spines: longer one about as long as basal width of claw, smaller one very slender and only about half as long.

**Ephippial female** (Figs 316, 317, 350-353, 355). Shape similar to that of parthenogenetic female (compare Figs 315 and 316, 347 and 350). Headshield much narrowed posteriorly, providing thereby more shell for the ephippium. Slough line very distinct, particularly ventrally (Figs 350, 352); toward ecdysial line bordered by small angular meshes (Fig.355), which obviously help in separation of anterior and ventral strip from ephippium on molting; these remain broadly attached at posterior end (Fig.352), forming 2 outward curving hooks or flaps. Inner lining of shell in ephippial region very darkly pigmented (Figs 316, 317), thereby obscuring any details underneath. Single ephippial egg. Surface of ephippium with closely packed tubercles, and even more closely packed in dimples that cover surface irregularly (Fig.353).

**Males.** *Instar-II* (Figs 337, 344, 364, 365, 367, 375). Body less high than in parthenogenetic female but otherwise similar in morphology (Fig.337). Postabdomen more slender than in female, but with same armament of marginal denticles and same clusters of setules along anal groove (Fig.344). Clusters of denticles oriented along length of postabdomen, not transversely diagonal to it. Lateral clusters of spinules in only specimen available visible in postanal portion but not elsewhere, seemingly similar to female; genital pore near base of claw but less close to it than in instar-III. Details of trunklimb I not visible. Rostrum shorter than in female, but with a similar weak evagination. Antennule with well developed anlage of male seta.

*Instar-III* (Figs 329, 338-343, 345, 346, 361-363, 366, 368-374). Body still lower relatively than in instar-II (Figs 338, 361). Portion of ventral margin anterior to midventral bulge sloping upward, straight, and with margin rolled inward, thereby obscuring ventral setae (Figs 338, 361); setae here have long, slender branches, creating a fuzzy appearance along this margin (Fig.362). Headshield shorter than in female, broad and roundly truncate at tip, provided with two stout denticles that arise submarginally and project beyond margin (Figs 340, 341, 368, 369). (Smirnov noted these and illustrated them in his drawings supposedly of *Pleuroxus jugosus*.) Antennules broader than in female, provided with very long male seta that is strongly brush-like distally (Figs 339, 369); antennular seta not quite so long, arising about one third from tip; seemingly only 9 aesthetascs. Trunklimb I with characteristic 3 IDL setae, plus large male seta (Fig.342); copulatory hook long and slender, with 3 crescentic ridges near tip (Figs 373-374). Postabdomen slender, and with preanal and postanal angles even less distinct than in female, but with relative lengths of the 3 zones about same as in female and with similar deployment of setular crescents and rows laterally, although with greater irregularity in placement (Figs 345, 346, 370-372); genital pore very near base of claw (Fig.372); about 13 denticles or denticle positions, mostly multiple and all heavily chitinised, those in proximal groups arranged obliquely; ventral margin flares outward basally (Figs 345, 346). Abdominal setae short, as in female. Distal tip of postabdomen narrowed and without claw stump or peduncle present in female. Postabdominal claw shorter and stouter than in female, strongly curved and provided with long setae along entire concave margin (Figs 345, 346, 366, 372); larger basal spine less than basal width of claw in length, smaller spine still smaller and not always easily visible.

**Length.** Females: overall 0.49-0.90 mm (n=137); instar-I 0.49-0.58 mm (n=25); instar-II 0.60-0.68 (n=54);

first embryos at 0.68 mm; ephippial 0.77-0.90 (n=13). Males: instar-II 0.63-0.65 (n=2); instar-III (= mature) 0.63-0.70 mm (n=15).

### *Plurispina multituberculata* n.sp.

Figs 376-402

**Etymology.** From (L) *multus* many, and (L) *tuberculum* tubercle, referring to the densely packed tubercles on the shell and head.

**Remarks.** Although only parthenogenetic females are available for this taxon, thereby precluding a complete description of its morphology, it seems to belong to the same genus as *Plurispina chauliodus*, with 10, 10, 7 and 5 setae in the gnathobasic filter combs of trunklimbs II-V, respectively, and in the general pattern of its morphology. The following characters differentiate it from its congener: 1) the shell is completely covered with radiating ridges and large, densely packed tubercles; 2) the tip of the rostrum is bead-like, rather than weakly bifid; 3) the labrum is elongate, rather than short and broad; 4) the smaller seta on the ODL is not strongly brush-like, possibly weakly so; 5) the anal groove is relatively much shorter, only about as long as the preanal portion instead of as long as the postanal portion; and 6) the rounded scallops in the distal portion of the preanal region are fewer and less well developed. Males and ephippial females are needed to define this taxon precisely. Because the type locality of this taxon is in the same general region of extreme south-western Australia as that for *Plurispina chauliodus*, and because the two species are from essentially the same kind of small pools in granite bedrock, it seems likely that there may well be a whole suite of related species of this genus or of other genera that could be discovered with intensive investigation. Smirnov & Timms (1983) have this sample listed as number 423 in their treatment of *Pleuroxus jugosus*.

**Material examined.** *Type locality.* Pool in granite, Dutarning Range, south of Perth, WA (Bayly, 1982: fig. 6), collected 24 June 1977 by I.A.E. Bayly, his field number 66.

**Types.** All 48 specimens plus exuviae from Bayly's sample 66 from the type locality. HOLOTYPE – a mature parthenogenetic female 0.81 mm long, mounted on a slide in glycerine jelly, AM (P39481). PARATYPES – a mature parthenogenetic female and an instar-I female mounted in glycerine jelly under the same coverslip have been deposited in each of the following museums: NMNZ (Cr. 6436), BM(NH) (1989.623), and the USNMNH (242123). All the remaining specimens and exoskeletal parts are in the Frey collection in Bloomington.

**Diagnosis.** Presence of 10, 10, 7 and 5 spines in gnathobasic filter combs of limbs II-V and general morphology put this taxon in the genus *Plurispina* along with *P. chauliodus*. Animal almost as high as long; strong keel beginning immediately after posterior headpore; shell covered with radiating ridges; head and shell covered with densely packed tubercles, providing a marked opaqueness; ventral margin with mean of 122 marginal seta (n=6), terminating at a small triangular tooth, followed by submarginal row of small but blunt setae along posterior margin. Eight long swimming setae. Tip of rostrum bead-like. Labrum elongate and narrowly rounded at tip. Postabdomen elongate; preanal portion and anal groove subequal in length, both much shorter than postanal portion; ventral margin strongly flared out in anterior third; long slender marginal denticles, irregularly arranged, but few fine setae associated with them. Postabdominal claw rather thick, provided with a row of long, stout setae along concave margin; 2 basal spines, longer one about as long as basal width of claw, other one very slender and much shorter.

**Parthenogenetic female.** *Shape and shell* (Figs 376-378, 395-397). Almost as high as long; rostrum short; strong keel beginning immediately after posterior headpore (Fig.400). Shell covered everywhere with series of prominent radiating or sloping ridges (Figs 376-378, 395) and a reticulation-like pattern on head and shell; entire head and shell covered densely with rounded tubercles of various sizes (Figs 380, 396, 398, 400); these line up in rows along anterior ridges, producing an effect similar to striae in other species. Posterior-dorsal angle completely absent, i.e., no appreciable change in curvature; posterior-ventral angle weakly developed, with 1 or 2 small bluntly triangular denticles, followed by submarginal row of stout setules extending toward posterior-dorsal angle (Fig.397). Head in lateral contour bulged out slightly over compound eye, with noticeable expansion behind posterior pore (Fig.377), produced by beginning of keel. Ventral setae 122 (range 116-127, n=6), including 9-11 arising internally along line roughly paralleling anterior margin. Shell brownish in colour, relatively opaque from tubercles.

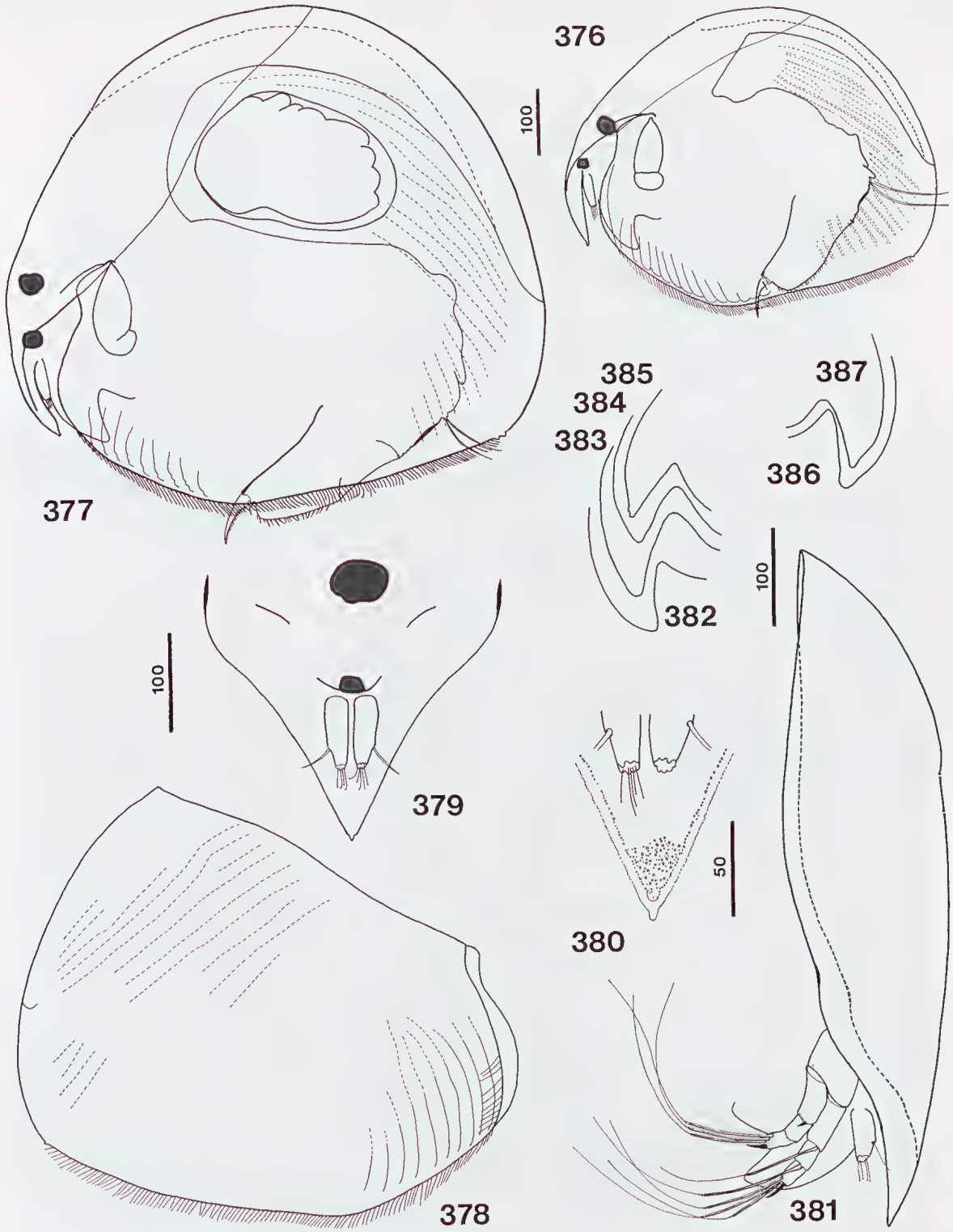
*Head* (Figs 379-381, 396, 398, 400). Rostrum about one third length of headshield (Fig.381); tip developed as small rounded point, somewhat separated from rest of rostrum (Figs 380, 398); edge rough from tubercles, but in plane view surface tubercles come out to row paralleling margin and do not occur between here and margin (Fig.380); no other markings; IP distance roughly 54 µm; PP distance 6.8 times IP distance; minor pores only about 1 major pore diameter apart.

*Antennule* (Figs 379-381). Slender but rather short, and with rounded backward extension at base; 9 aesthetascs, about one third length of antennule; antennular seta about half as long as antennule, arises from a notch or cup about one third from tip; aesthetasc field surrounded by blunt triangles.

*Antenna* (Figs 381, 398). Formula: 0(1)-0-3(1)/1-1-

3(1). Eight long swimming setae; seta from basal segment of exopodite about two thirds length of longest natatory seta; 1 terminal seta from tip of each branch slightly shorter than other 2. Terminal spines on each branch long and well developed.

*Labrum* (Figs 382-387). Rather narrow blade, with tip moderately narrowed, rounded, not attenuated; anterior margin mostly evenly curved, sometimes with slight concavity or irregularity near tip; posterior margin usually weakly concave; angle considerably less than

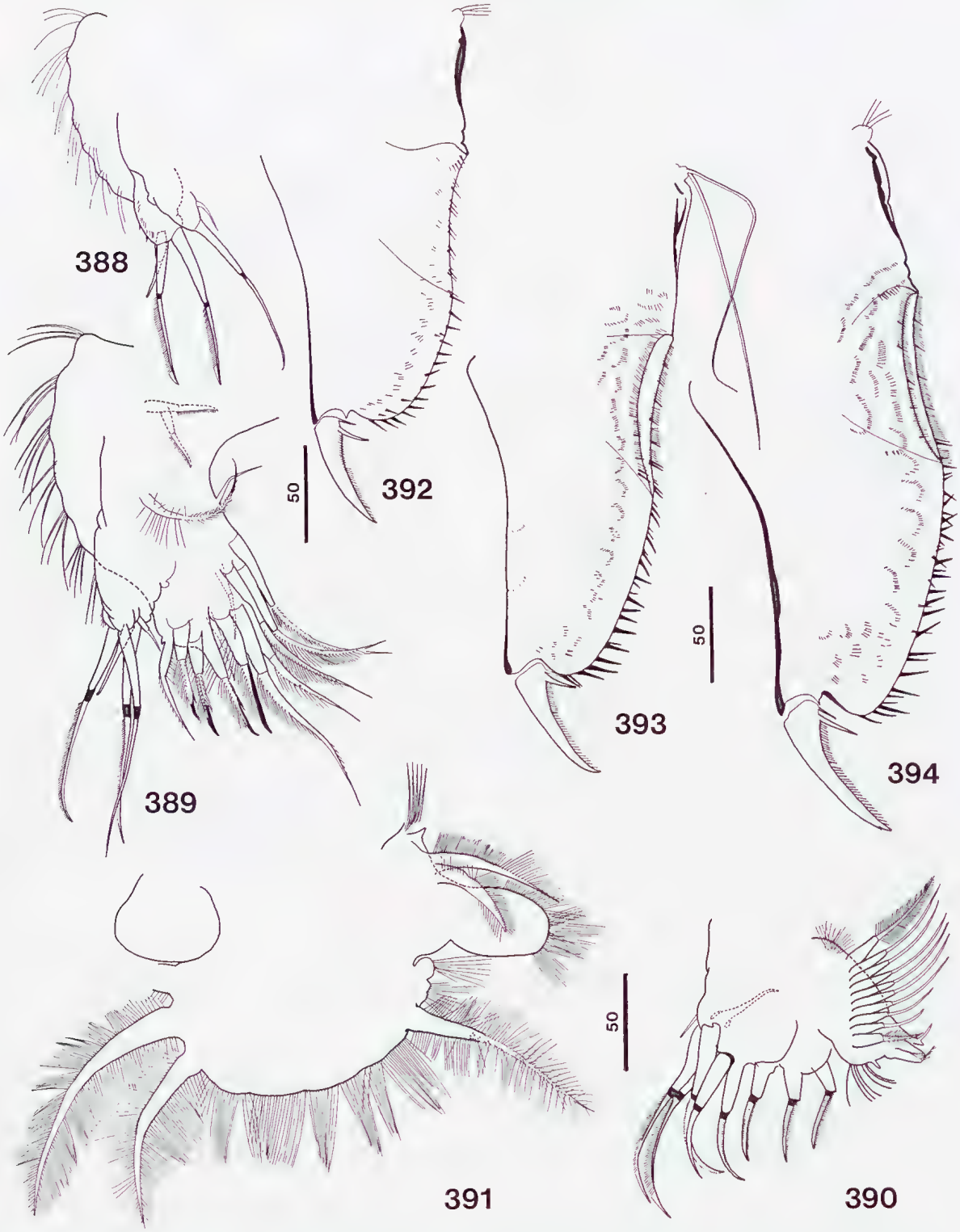



**Figs 376-387.** *Plurispina multituberculata* n.sp. All specimens parthenogenetic PARATYPES from Bayly sample 66 (granite pool in Dutarning Range south of Perth, WA, 24 June 1977). 376. instar-I female; 377. parthenogenetic female; 378. shell of instar-I female; 379, 380. rostrum and antennules of parthenogenetic female (number 380 shows general distribution and size-range of tubercles near tip of rostrum); 381. headshield of parthenogenetic female, with antennule, antenna, and labrum (note change in curvature behind posterior headpore from initiation of keel); 382-387. labra of parthenogenetic females.

90°, rather narrow.

*Trunklimb I* (Figs 388, 389, 399). Two ODL and 3 IDL setae; long ODL seta and 2 long IDL setae about same length; smaller ODL seta less than half as long as basal segment of longer seta, seemingly without any brush-like setules in distal segment; smaller IDL seta apparently without setules; tip reaches setulate zone of other 2 setae; lateral seta arising near base of ODL-IDL ridge well developed, openly brush-like. Accessory seta of middle and posterior groups of corm seta well developed; middle seta of middle group much the longest.

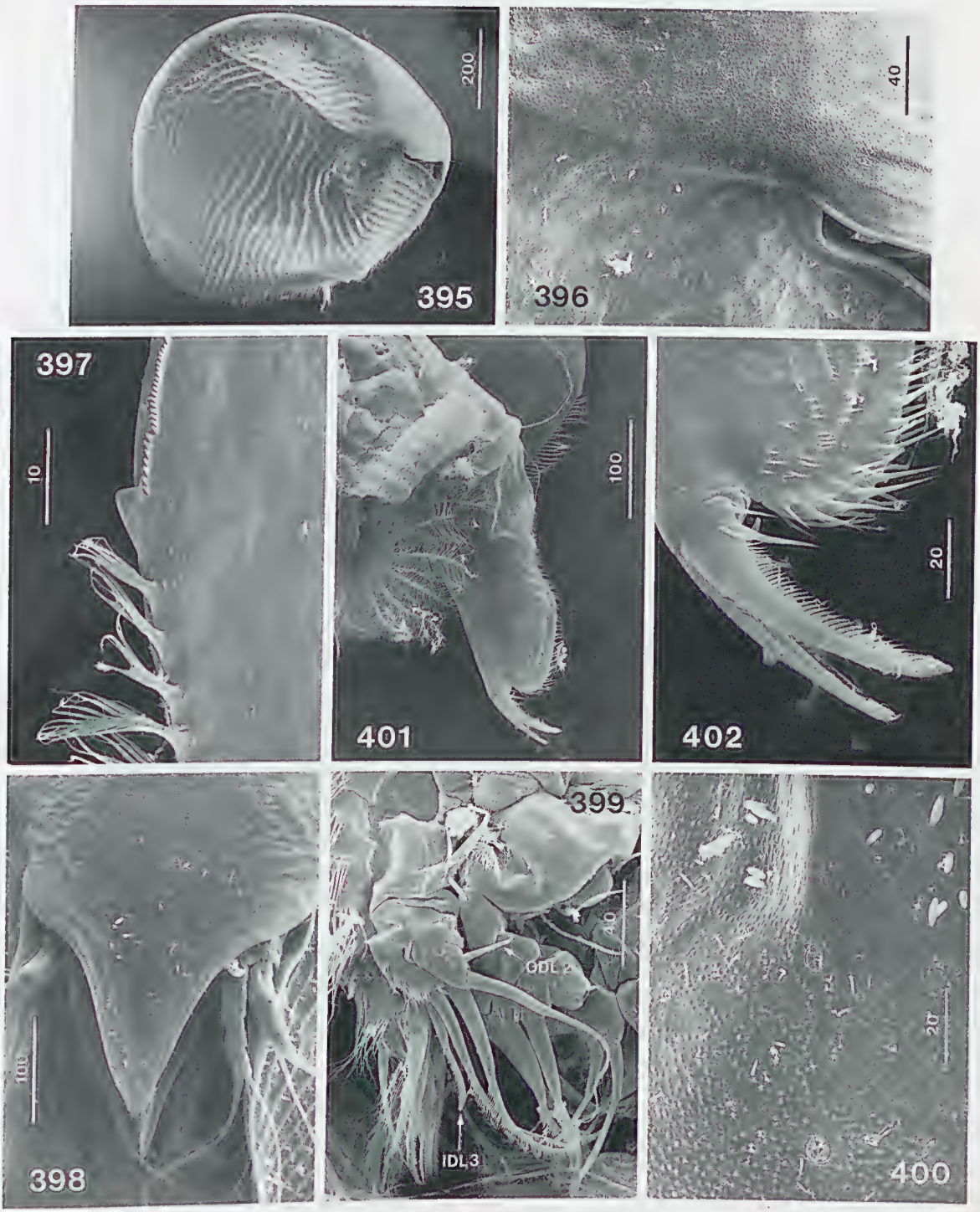
*Trunklimb II* (Fig.390). Ten setae in gnathobasic filter comb; all scraping spines with row of distinct spinules in distal segment; about 7 thick, curved setae between gnathobase and scraping spines.




**Figs 388-394.** *Plurispina multituberculata* n.sp. All specimens parthenogenetic PARATYPES from Bayly sample 66 (granite pool in Dutarning Range, WA, 24 June 1977). 388, 389. trunklimb I (NB: ODL2 is not feathered); 390. trunklimb II; 391. trunklimb V; 392. postabdomen of instar-I female; 393, 394. postabdomen of mature female.

*Trunklimbs III-V* (Fig.391). Ten, 7 and 5 setae in gnathobasic filter comb, respectively, and 7, 7 and 4 feathered exopodite setae. On trunklimb III, distalmost 2 'hard' setae slender, heavily chitinised, and either without setules or else extremely small; these project ventrally in intact animals. Soft setae of trunklimb IV close together, leaving long free margin on exopodite toward respiratory bulb.

*Postabdomen* (Figs 392-394, 401). Ventral margin straight distally, expanded outward at basal third; dorsal margin with both angles weak and almost absent; anal groove shallowly concave. Preanal portion and anal groove subequal in length, both much shorter than postanal portion. Postanal portion with irregular array of long slender denticles, which change orientation in basal half, creating confusing configuration; all thickly




**Figs 395-402.** *Plurispina multituberculata* n.sp. All specimens parthenogenetic PARATYPES from Bayly sample 66 (granite pool in Dutarning Range, WA, 24 June 1977). 395. parthenogenetic female; 396. shell-headshield junction, showing distribution of tubercles; 397. posterior-ventral angle and adjacent portion of posterior margin of shell, from inside; 398. rostrum and antennae; 399. trunklimb I, showing long but unfeathered ODL2 seta and relatively long IDL3 seta; 400. headpores and beginning of keel; 401. postabdomen; 402. tip of postabdomen and postabdominal claws.

chitinised, with few thin setae mixed in; often accessory denticles, sometimes arising laterally rather than with major denticles; no organisation into distinct groups of denticles, except occasionally basally, and these not positioned transverse to margin. Anal groove with 6 or 7 clusters of setae, each in a row, with tips extending well beyond margin, distalmost seta of each group thicker than other (Figs 393, 394); these probably derive from diagonal clusters of 2-3 seta each in instar-I individuals (Fig.392). Lateral surface of postanal portion with row of crescentic groups of setae, and with some additional groups distally, and along anal groove and in preanal region. Two curved rows of setules across ventral margin. Two or 3 weak indentations in distal part of preanal margin. Abdominal setae quite long, reaching to about two thirds of anal groove when extended.

*Postabdominal claw* (Figs 392-394, 402). Stout distally, with 2 successive rows of long, stout setae along concave margin. Two basal spines, longer one as long as basal width of claw, smaller one more slender, about half as long.

**Length.** Overall 0.50-0.88 mm (n=48); instar-I 0.50-0.59 mm (n=19); instar-II 0.61-0.72 mm (n=12); smallest female with eggs 0.73 mm.

### *Pleuroxus helvenacus* n.sp.

Figs 403-434

**Etymology.** From (L) *helvenacus* pale yellow, yellowish, from the general appearance of the specimens.

**Comments.** Although *Pleuroxus helvenacus* in many respects resembles the two species in the new genus *Plurispina* described in this paper, it is retained in the genus *Pleuroxus* because of its 8, 8, 6 and 4 setae in the gnathobasic filter combs of trunklimbs II-V, respectively.

**Material examined.** *Type locality.* Flooded meadow near Mount John, South Island, New Zealand, collected 20 Mar. 1987 by D.G. Frey, Frey accession number 8374. The meadow is 3.1 km from the highway along the road on the west side of Lake Tekapo.

*Other locality.* Tekapo pond 8A, in the same general region as type locality, collected 15 Oct. 1980 by C.W. Burns.

**Types.** All specimens and exuviae from the type locality, amounting to 19 specimens plus many shells and headshields with appendages. HOLOTYPE – a mature parthenogenetic female 0.74 mm long, mounted on a slide in glycerine jelly, NMNZ (Cr. 6437). PARATYPES – a mature parthenogenetic female on a slide in glycerine jelly has been deposited in each of the following museums: AM (P39482), BM(NH) (1989.624), and the USNMNH (242124).

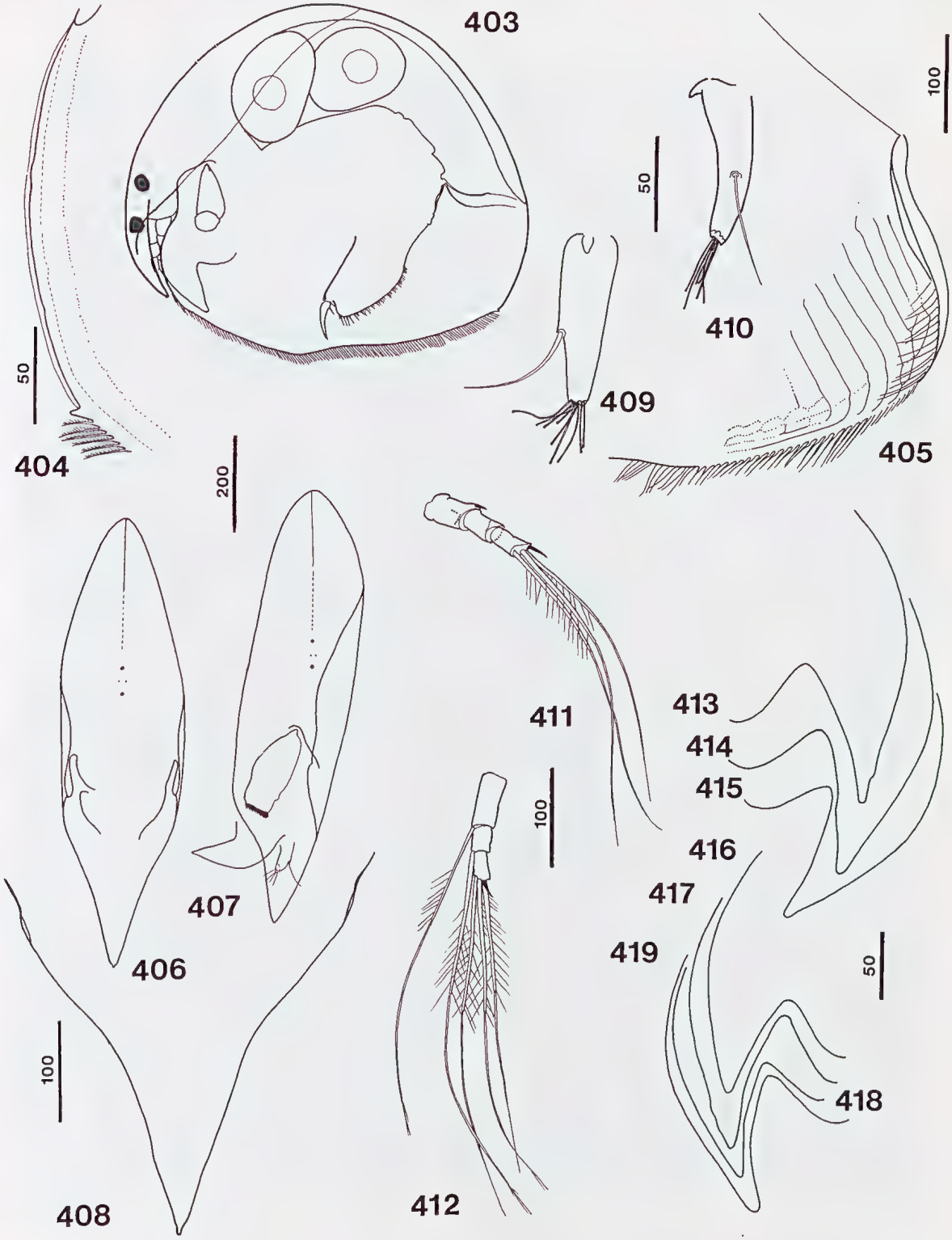
All the remaining specimens and exoskeletal parts from the type series, plus 17 specimens recovered from the Tekapo pond, are in the Frey collection in Bloomington.

**Short diagnosis.** Almost as high as long; ventral margin weakly curved, provided with a mean of 118 marginal setae, those in posterior three fifths being densely feathered on outside; single rounded tooth (range 0-2) at posterior-ventral angle; entire shell and head covered with small rounded tubercles; about 8 short, curved striae at anterior end of shell; no keel present but instead a rather sharp ridge; light yellowish colour, without pigmentation. Labrum long, narrow, finely rounded at tip. Antennule slender, tapered to narrow tip; antennular seta arising one third from tip, longer than half of antennule; aesthetasc field surrounded by pyramidal tubercles. Antenna with 8 swimming setae, all almost equally long; basal segment and rami provided with transverse rows of spinules. Nothing distinctive about trunklimbs, except unusually long seta on exopodite of limb III. Postabdomen unique; about 20 marginal denticles or positions in postanal region, distally almost touching one another at base, proximally multiple, either as several equally developed denticles or 1 denticle and adjacent row of long setae; preanal length less than anal length, which is less than postanal; distal third of preanal portion single, with several chevron-like thickenings across margin; preanal angle reasonably distinct, postanal one obscured.

**Parthenogenetic female.** *Shape and shell* (Figs 403-405, 420, 427-430). Body almost as high as long; dorsal margin evenly curved from tip of rostrum to posterior-ventral angle (posterior-dorsal angle almost completely absent); posterior margin short, weakly but evenly convex; ventral margin with weak bulge just anterior to midpoint, provided along entire margin with 118 setae (range 108-126, n=19), including about 12-15 long setae bent inward at anterior end (Fig.405), those in posterior three fifths strongly feathered laterally along posterior edge (Fig.430), those in anterior two fifths relatively unfeathered; about 8 short striae anteriorly, roughly paralleling anterior margin, with a series of radiating ridges posteriorly; most distinctive are the many fine tubercles scattered over entire shell (and head) (Figs 428, 429), sometimes organised into lines outlining meshes (Fig.405), as in central region of shell and along ventral edge; above tips of ridges and on head are many small depressions or dimples (Fig.428); dark line closely paralleling posterior margin (Fig.404). Generally 1 rounded tooth [0(4), 1/2(1), 1(28), 1 1/2(3), 2(9)] at posterior-ventral angle (Figs 404, 430), followed by row of marginal setae, which quickly become submarginal, extending toward posterior-dorsal angle. Body laterally compressed, narrow from side to side, tapering to a median ridge (not a keel) dorsally, beginning shortly behind head pores. Colour light yellowish, clear, no pigmentation.

*Head* (Figs 406-408). Headshield long, relatively narrow. Rostrum long, rather sharply tipped and with fine button-like extension; held close to body. IP distance averages 56 µm ; PP distance 5.4 times IP; minor pores more than 2 pore diameters apart. Median longitudinal ridge beginning shortly behind headpores.

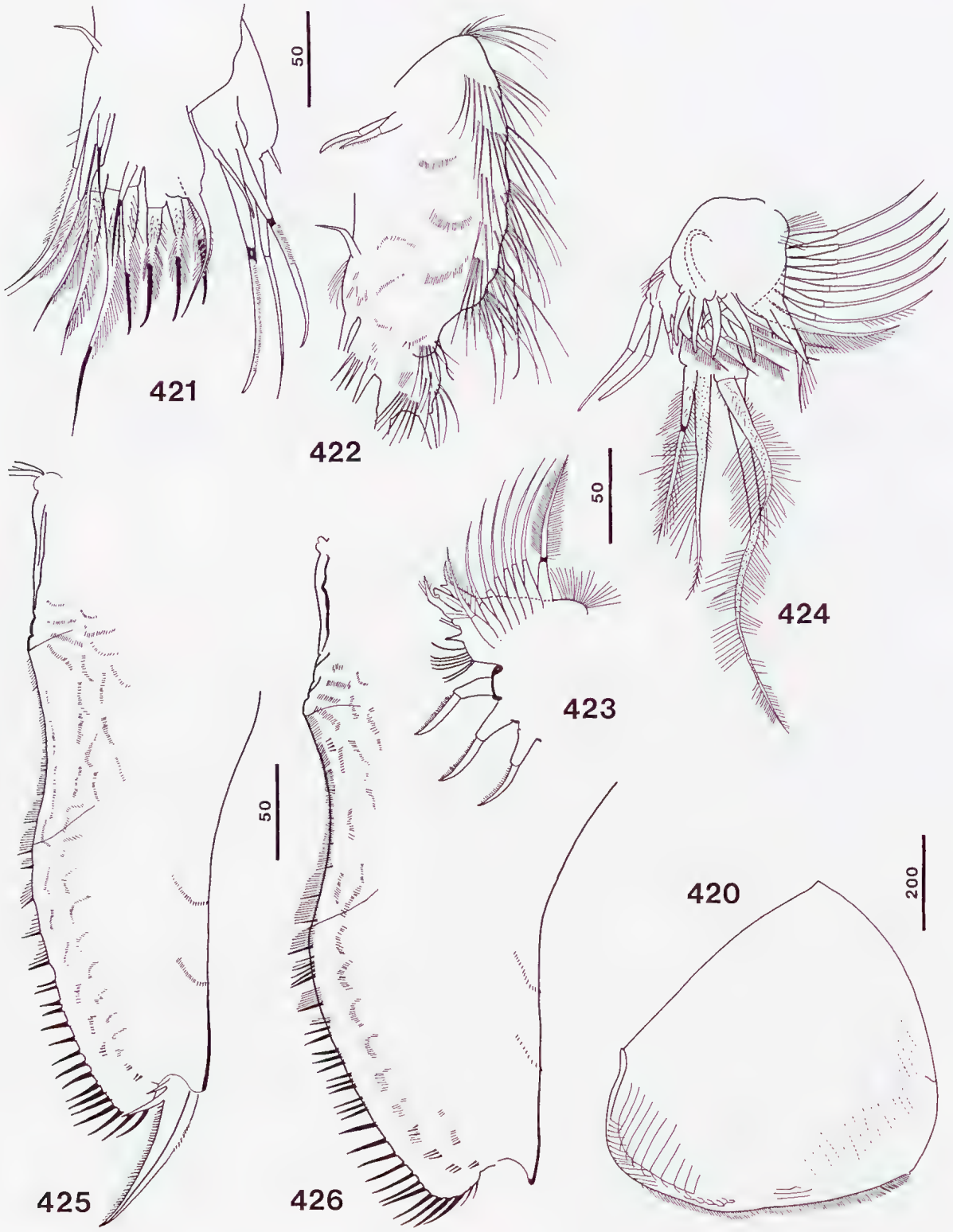
*Antennule* (Figs 409, 410, 431). Long, slender, tapered distally to narrow tip that is provided with pyramidal




**Figs 403-419.** *Pleuroxus helvenacus* n.sp. All specimens parthenogenetic PARATYPES from Frey sample 8374 (flooded meadow near Mount John, South Island, NZ, 20 Mar. 1987). 403. parthenogenetic female; 404. posterior-ventral angle and posterior margin of shell; 405. anterior portion of shell; 406-408. headshield; 409, 410. antennule; 411. exopodite of antenna; 412. endopodite of antenna; 413-419. labra.

tubercles at edge; base with a short backward expansion that is narrowly rounded at tip (Fig.431). Nine slender aesthetascs, about one third length of antennule; antennular seta half as long as antennule, arising one third from tip.

*Antenna* (Figs 411, 412). Eight long swimming setae, the one from basal segment of endopodite almost as long as others; one of terminal setae on each branch only very slightly shorter than other 2; all basal segments provided with numerous setules laterally. Terminal spines

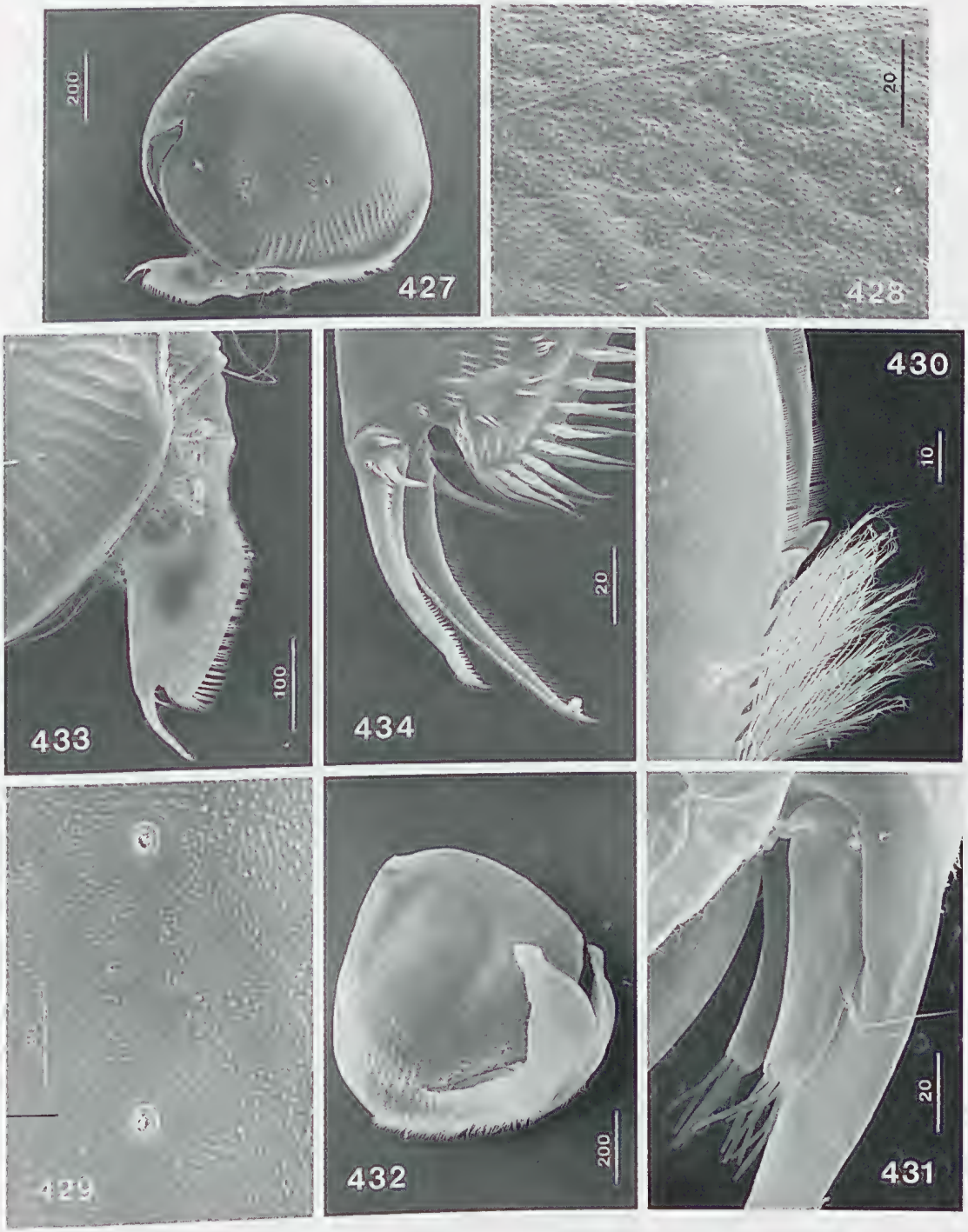



**Figs 420-426.** *Pleuroxus helvenacus* n.sp. All specimens parthenogenetic PARATYPES from Frey sample 8374 (flooded meadow near Mount John, South Island, NZ, 20 Mar. 1987). 420. shell; 421, 422. trunklimb I; 423. gnathobase and three scraping spines of trunklimb II; 424. trunklimb III, showing the one very long exopodite seta; 425, 426. postabdomen and postabdominal claw.

less than half length of terminal segments; spine from basal segment of exopodite very small. All segments of both branches of antenna with transverse median and distal rows of fine spinules.

*Labrum* (Figs 413-419). Labral keel elongate, tapered to narrow, rounded tip; anterior margin relatively straight toward tip, sometimes with notch or waviness near tip; posterior margin usually weakly concave, sometimes almost straight; posterior angle narrow, considerably less than 90°.

*Trunklimb I* (Figs 421-422). Two ODL setae, smaller one short but distinct, unfeathered; 3 IDL setae, shortest one evenly tapered, bluntish at tip, not reaching distal ends of basal segments of 2 long setae. Middle




**Figs 427-434.** *Pleuroxus helvenacus* n.sp. All specimens PARATYPES from Frey sample 8374 (flooded meadow near Mount John, South Island, NZ, 20 Mar. 1987). Specimen 432 is an ephippium, all others mature parthenogenetic females. 427. parthenogenetic female; 428. dimples and tubercles at shell-headshield boundary; 429. headpores and tubercles (note distance apart of minor pores); 430. posterior-ventral angle with tooth, plus shell margin and setae on either side; 431. antennules (note backward extension at base); 432. ephippium; 433,434. postabdomen and postabdominal claws (note that distal denticles on postabdomen are all single and close together).

seta of middle group of corm setae much the longest. All 3 accessory setae well developed. Long, delicate lateral setae arising laterally from base of ODL-IDL ridge.

*Trunklimb II* (Fig.423). Short seta on margin between gnathobasic setae and scraping spines, with 2 long setae toward gnathobasic setae, and 7 or 8 stout curved setae toward scraping spines. Scraping spines 1-3 considerably shorter than number 4; first 7 setae provided with row of slender setules along distal segment; 8 setae in gnathobasic filter comb.

*Trunklimbs III-V*. Setae in gnathobasic filter comb number 8, 6 and 4 (3 in one specimen), respectively, and number of soft setae on exopodite 7, 7 and 4, respectively. No striking differences in morphology, although longest exopodite seta of limb III is longer than usual (Fig.424).

*Postabdomen* (Figs 425, 426, 433, 434). Elongate and broad; preanal portion less than anal portion which is less than postanal. Ventral margin flared outward proximally, 2 curved rows of spinules embracing margin. Postanal margin with about 20 denticles or denticle positions; distal denticles almost touching at bases; proximal ones multiple, either as several strong setae or as one or a couple strong setae distally and several long setae proximally; anal groove armed with about 7 successive groups of long setae, each group typically ending in a stouter seta distally, and all groups tending to project well beyond margin; single row of spinular crescents laterally along dorsal margin, with a few additional groups distally, and many additional groups proximally and in preanal region. Preanal angle reasonably distinct; postanal angle obscure, rounded. Several transverse, chevron-like folds in distal third of preanal region; proximal two thirds expanded somewhat laterally. Abdominal setae quite long, reaching to about middle of anal groove when extended.

*Postabdominal claw* (Figs 425, 434). Slender; evenly tapered and evenly curved. Two basal spines, longer one curved outward away from claw, longer than basal width of claw, shorter one straight, more slender, about half as long. Row of long setae along concave margin, plus row along medial surface that project beyond concave margin.

**Ephippium** (Fig.432). Just one ephippium was found, which is typical for the chydorine anomopods in its morphology. Anterior and ventral parts of shell that peel away from ephippium anteriorly remain broadly attached near posterior end. Surface sculpturing a series of angular tubercles, each with several lines or ridges radiating outward.

**Length.** *Type population.* Overall 0.52-0.88 mm (n=19); instar-I 0.52-0.60 mm (n=10); mature 0.73-0.88 mm (n=9); smallest female with eggs 0.76 mm. Tekapo pond 8A: overall 0.57-0.89 mm (n=17); instar-I 0.57-0.59 mm (n-3); instar-II 0.62-0.71 mm (n=6); mature 0.76-0.89 mm (n=8); smallest female with eggs 0.78 mm.

## *Planicirclus* n.gen.

**Type species.** *Planicirclus alticarinatus* n.sp. by original designation.

**Etymology.** From (L) *planus* flat, and (L) *circlus* a circle or circular body (masculine gender), referring to the general shape of the taxon.

**Remarks.** This taxon from Western Australia is by far the largest in size among the *Pleuroxus*-like group of species. Many of its characters that seem unique may be related to its large size. Thus, the PP distance is extremely long - about 13 IP distances; the ventral setae on the shell average 186, which is much greater than for any other species; the eye and ocellus are very small relative to the size of the animal and are very close together; and there are up to 25 curved striae in the anterior part of the shell, many more than in any other species. On the other hand, there are some truly distinctive characters: there is a long secondary seta on the ODL, longer than in *Plurispina*, which is strongly brush-like in the distal segment; the middle and posterior setae of the middle group of corm setae are almost equally long, the middle seta being only slightly longer; there are very many setular crescents on the sides of the postabdomen; and there are two resting eggs in the ephippium. The setae on the gnathobasic filter comb of trunklimbs II-V number 8, 8, 6 and 4, respectively, which is typical for most *Pleuroxus* and *Pleuroxus*-like species from Australia and New Zealand. Deciding which of these characters are generic characters will have to await the finding of a second species in the genus. The taxon seems most closely related to *Pleuroxus helvenacus* from New Zealand in the shape of the postabdomen and its large number of marginal denticles, and in the regular, attenuated shape of the labrum, but the smaller ODL seta of *Pleuroxus helvenacus* is much different, and the middle seta of the middle group on the corm is much the longest. Resolution of the significance of these similarities and differences will have to wait until males and ephippial females of the New Zealand taxon become available.

## *Planicirclus alticarinatus* n.sp.

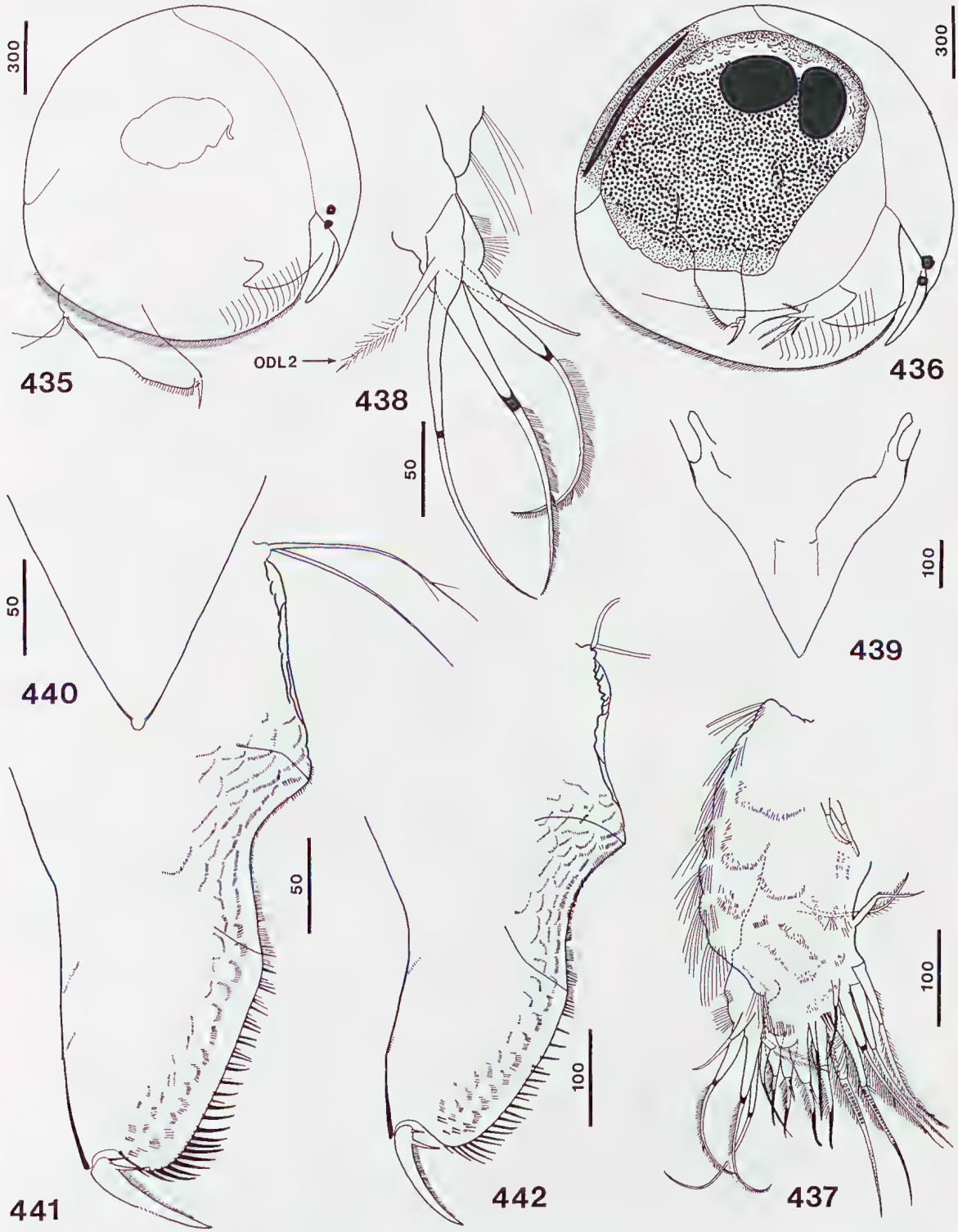
Figs 435-488

**Etymology.** From (L) *altus* high, deep, and (L) *carina* a keel, referring to the broad keel on the head and shell.

**Material examined.** *Type locality.* Cracker's Swamp, 210 km north of Perth and 4.8 km west of Brand Highway, collected by R.J. Shiel on 30 Sept. 1981, his accession number 792 (field number W.A. 4). Dark

humic water, less than 30 cm deep. Conductivity 800 µS $cm^{-1}$

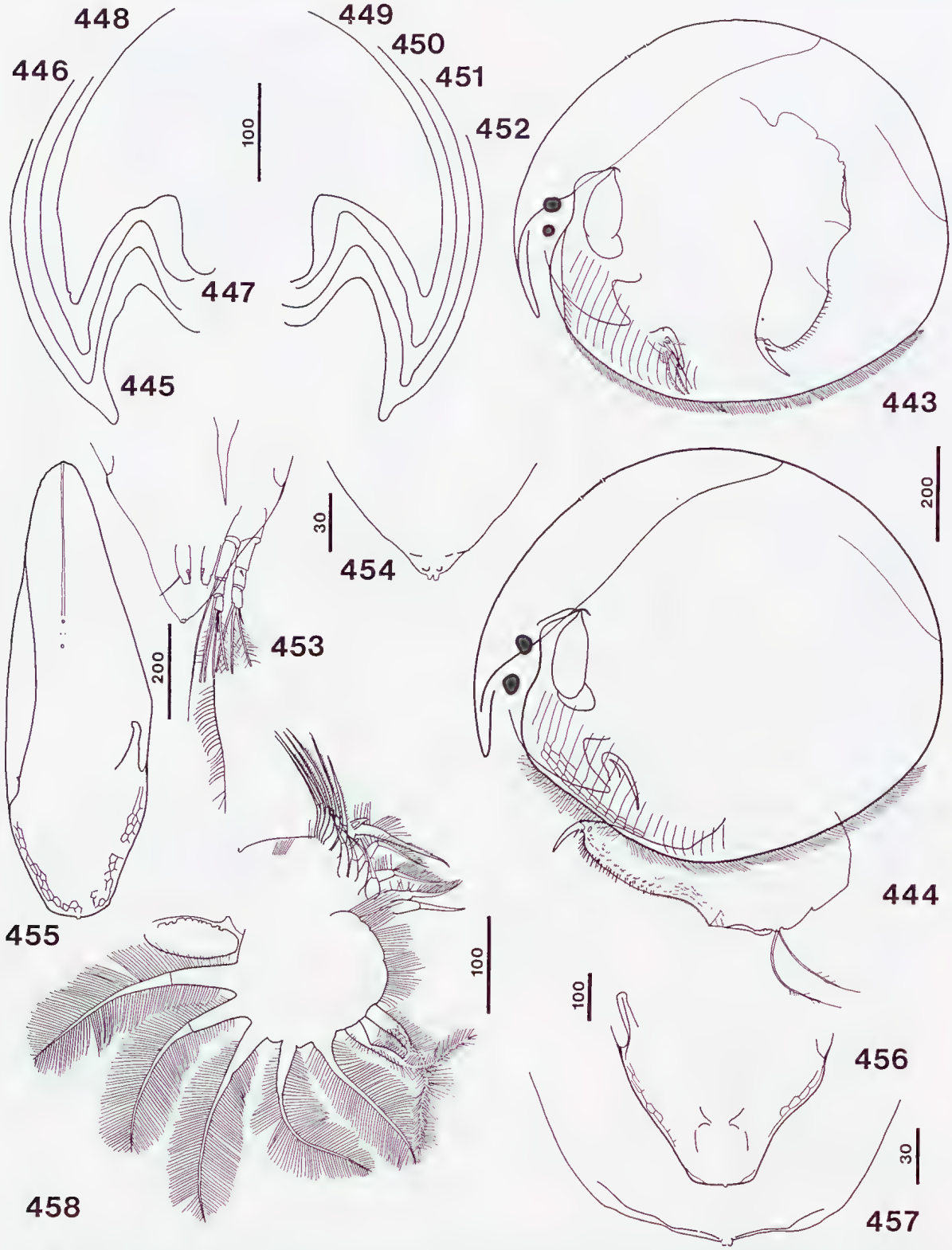
**Types.** 111 specimens, plus numerous heads, shells, and some exuviae from type locality. HOLOTYPE – a mature parthenogenetic female 1.23 mm long, mounted on a slide in glycerine jelly, AM (P39483). ALLOTYPE – a mature male 1.07 mm long, mounted on a slide in glycerine jelly, AM (P39484). Special PARATYPES – mounted separately on slides in glycerine jelly, AM: an ephippial female 1.37 mm long (P39485); an instar-I male 0.75 mm long (P39487); an




**Figs 435-442.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792 (Cracker's Swamp, 210 km north of Perth, WA, 30 Sept. 1981). 435. parthenogenetic female; 436. ephippial female (note two ephippial eggs); 437. 438. trunklimb I, showing subequal lengths of middle and posterior setae of middle group of corm setae, and large size and brushy distal segment of ODL2; 439, 440. rostrum, with button-like tip; 441, 442. postabdomen of parthenogenetic female.

instar-II male 0.87 mm long (P39486). PARATYPES – 1 slide each containing a mature parthenogenetic female, an ephippial female, an instar-I male, an instar-II male, and a mature male, mounted separately in glycerine jelly, have been deposited in the following museums. The numbers are the catalogue or registration numbers of the specimens.

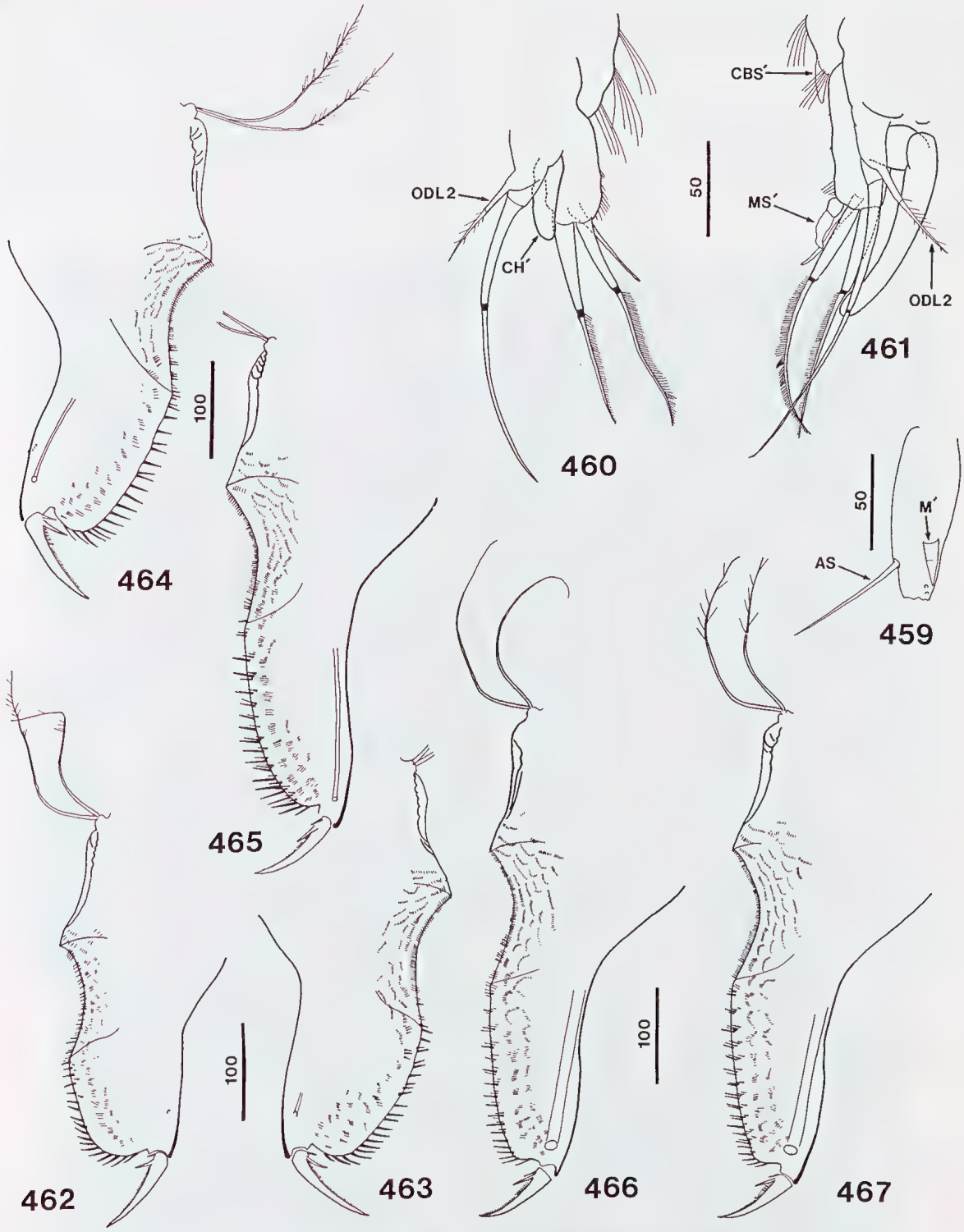
| | NMNZ | BM(NH) | USNMNH |
|---|---|---|---|
| Paratypes | | | |
| parthenogenetic female | Cr. 6438 | 1989.625 | 242125 |
| ephippial female | Cr. 6439 | 1989.627 | 242125 |
| instar-I male | Cr. 6440 | 1989.629 | 242125 |
| instar-II male | Cr. 6441 | 1989.628 | 242125 |
| mature male | Cr. 6442 | 1989.626 | 242125 |




**Figs 443-458.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792 (Cracker's Swamp, 210 km north of Perth, WA, 30 Sept. 1981). 443. instar-II male; 444. mature male; 445-452. labra of parthenogenetic females; 453, 454. bifid rostrum of instar-II male, with antennules and antenna; 455-457. headshield and rostrum with bifid button, mature male; 458. trunklimb IV of parthenogenetic female.

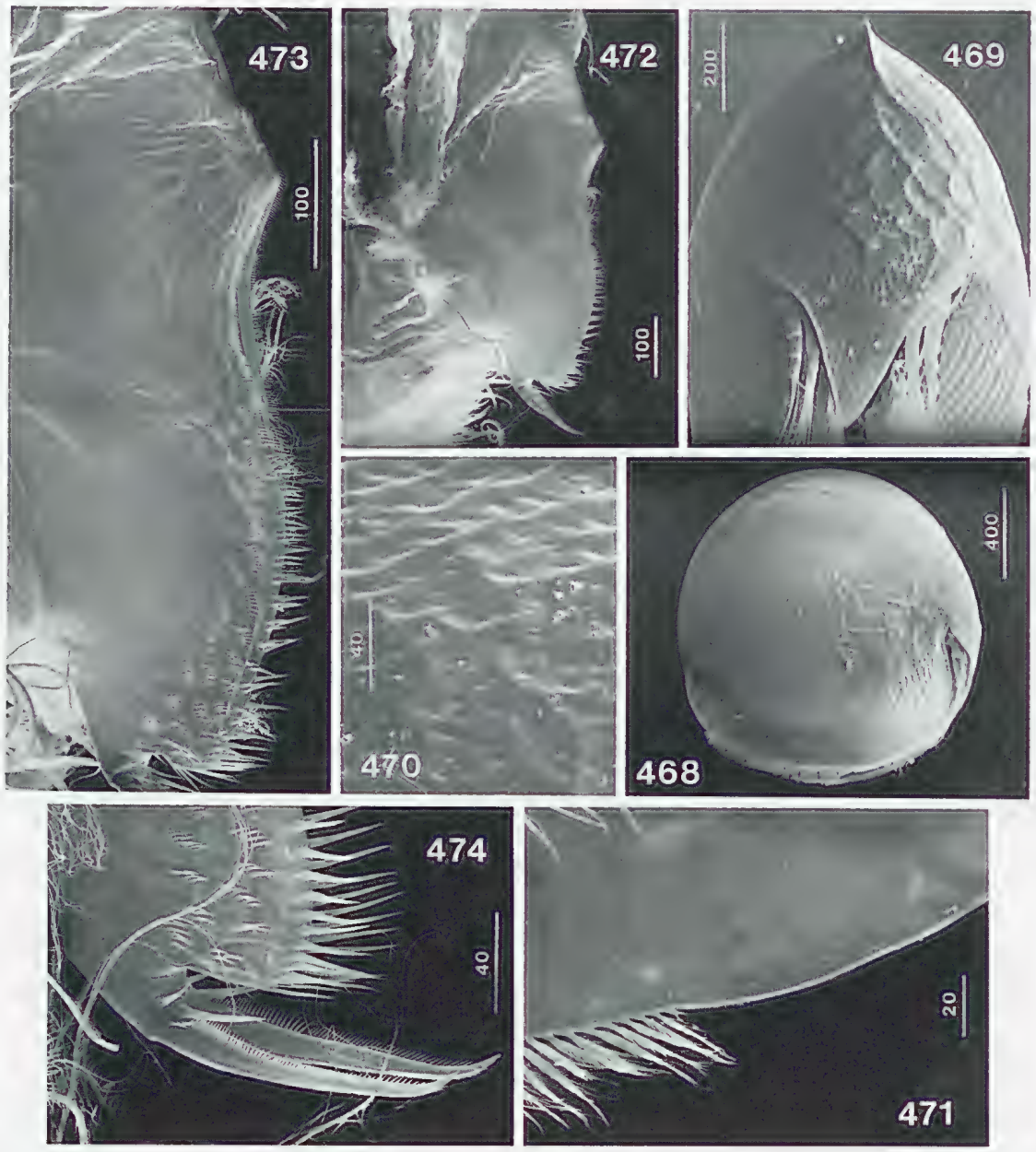
All the remaining paratypes are in the Frey collection in Bloomington.

**Diagnosis.** Highly distinctive taxon – large, almost circular in lateral outline, laterally compressed, with a high keel beginning just behind headpores, and with rostrum held close to body. PP distance very long, averaging 12.6 times IP distance. Mean of 186 ventral




**Figs 459-467.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792 (Cracker's Swamp, 210 km north of Perth, WA, 30 Sept. 1981). 459. antennule of instar-II male (note that anlage of male seta, M', is short and stout; antennular seta, AS, is long and arises only about 1/5 from end); 460. part of trunklimb I of instar-I male (CH', anlage of copulatory hook; ODL2, shorter seta of ODL, which in this species is very long and highly brush-like in the distal segment); 461. part of trunklimb I of instar-II male (CBS',anlage of copulatory brush seta; MS', anlage of male seta on IDL; ODL2, shorter ODL seta); 462. postabdomen of instar-I male; 463, 464. postabdomen of instar-II male; 465-467. postabdomen of mature male.

setae on shell, including those turned inward at anterior end. Entire surface of shell covered with ridges, cross connections, and scallops; about 15-25 anterior ridges paralleling anterior margin, with short striae. ODL has long second spine, strongly plumose in distal segment, as long as basal segment of longer ODL spine. Antennular seta long, arising one quarter from tip of antennule. Eight long swimming setae on antenna, shortest from basal segment of endopodite. Postabdomen with anal groove deeply concave, shorter than preanal and postanal portions, which are roughly subequal; postanal portion with about 20 denticles or denticle positions; denticles long, slender, somewhat curved toward anal groove, distal denticles close together at their bases; many spinular crescents along sides of postabdomen, particularly along anal groove and in preanal region; 2 crescents of fine setae across ventral margin of postabdomen. Setae in gnathobasic filter combs number 8, 8, 6 and 4 in limbs II-V, respectively. Males almost as nearly circular in outline as females. Instar-II male with stout anlage of male seta on antennule, arising about one third from tip; rostrum shorter and broader than in female, with two small denticles at tip. Mature male has long, brushy male seta on antennule; rostrum short, truncate, and with small emarginate globule arising subterminally at tip; anterior part of ventral margin of shell turned inward, with many long, very slender setae seeming to arise directly from shell; postabdomen more

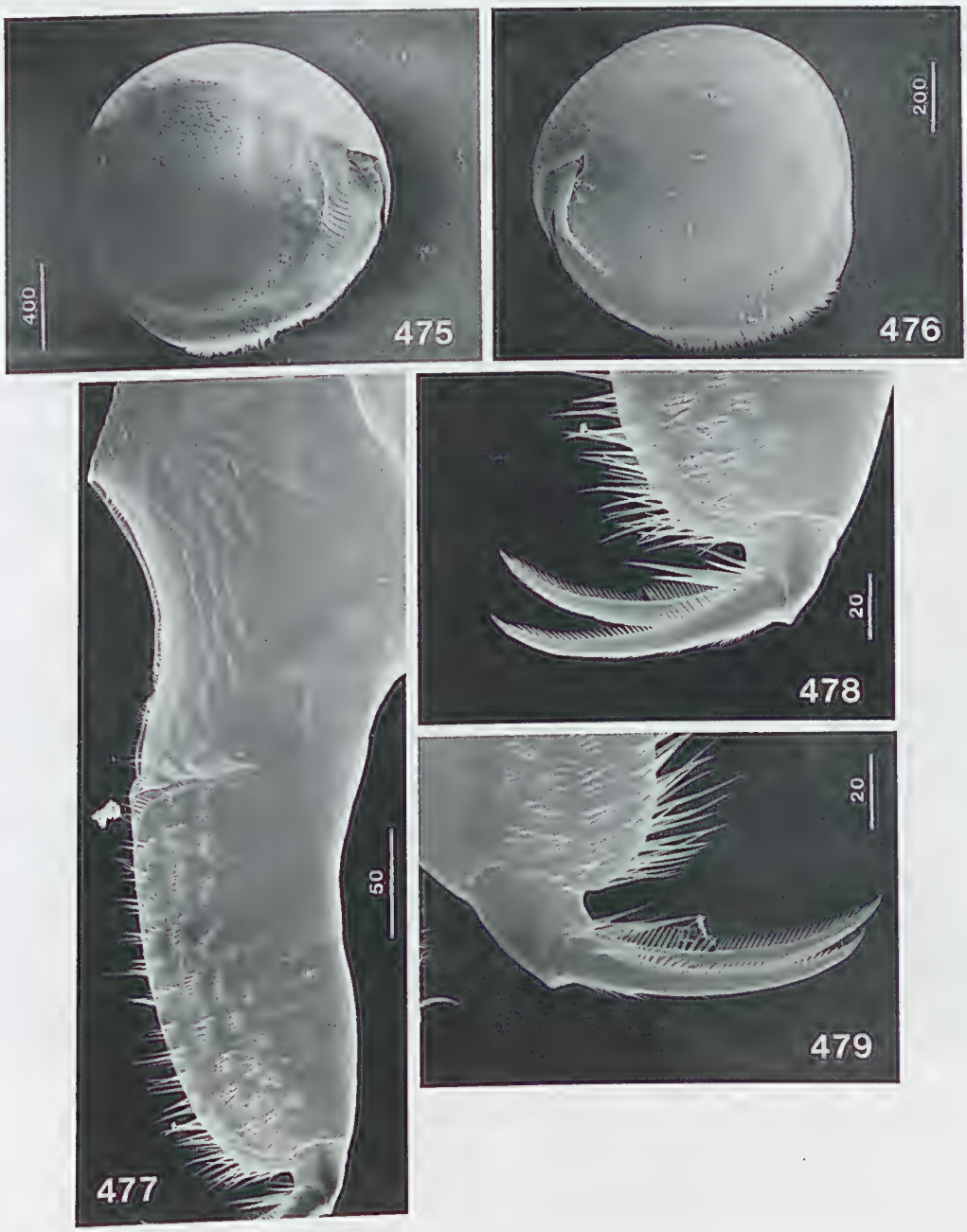



**Figs 468-474.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792. 468. parthenogenetic female; 469. anterior view of parthenogenetic female, showing rostrum, antennae, and strong keel beginning just behind posterior median pore; 470. sculpturing of shell of parthenogenetic female; 471. posterior-ventral region of shell of parthenogenetic female, showing complete absence of any denticle; 472-474. postabdomen and postabdominal claws.

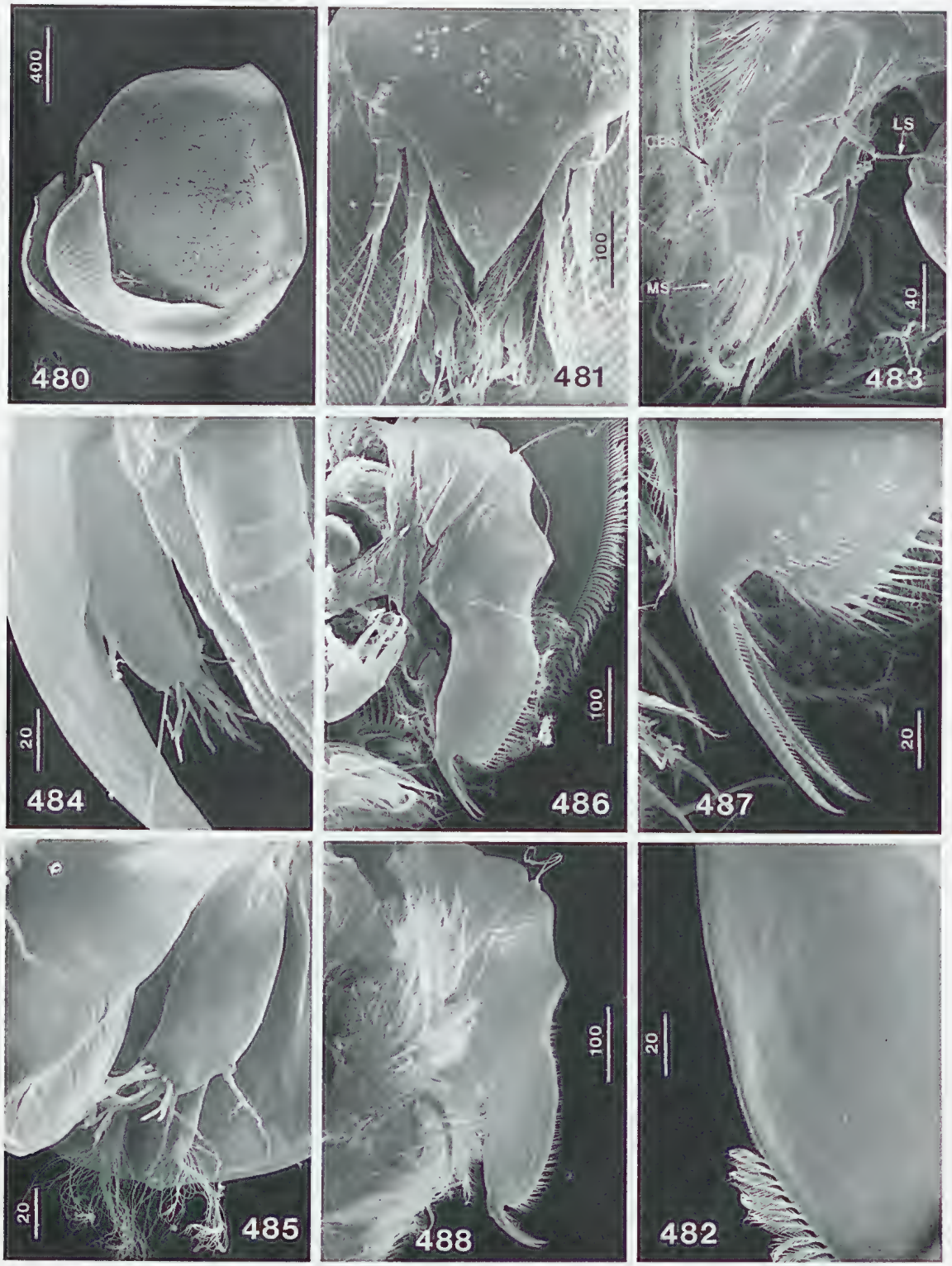
slender and elongate than in female; preanal angle sharp but very obtuse, and postanal angle rounded and inconspicuous; denticles mostly multiple, with groups arranged transversely or obliquely to margin; genital pore far distad, near base of peduncle for claw.

**Parthenogenetic female.** *Shape and shell* (Figs 435, 468-471). Disc-shaped, almost circular in lateral view, with ventral margin having much less curvature than dorsal margin; body strongly flattened from side to side, and with very sharp keel beginning directly behind posterior pore and continuing to posterior-dorsal angle. Series of 15-25 short, vertical striae on anterior part of shell, roughly paralleling anterior margin; elsewhere on shell are various ridges and reticulations - longitudinal ridges dorsally, reticulations ventrally and posteriorly; ventral portion of shell with irregular dimples and ridges; a mean of 186 marginal setae (range 167-203, n=20), including specimens of all stages and instars except mature males), including 10-12 at anterior end that turn inward from submarginal ridge; no tooth at posterior-ventral angle in any specimens (Figs 471, 482), but row of slender and short marginal-submarginal setae along posterior margin to posterior-dorsal angle. Shell surface irregularly dimpled (Fig.470). Rostrum held close to body; antennules and part of labrum obscured by antennae directed downward.

*Head* (Figs 439, 440, 469). Strongly convex, with




**Figs 475-479.** *Planicirclus alticarinatus* n.sp. All specimens PARATYPES from Shiel sample 792. 475. ephippial female (note distinctness of slough line); 476. instar-II male; 477. postabdomen of mature male; 478, 479. tip of postabdomen and postabdominal claws of mature male (note distinct angle at the ventral tip of the caudal peduncle, and long, straight nature of basal spines).




**Figs 480-488.** *Planicirclus atlicarinatus* n.sp. All specimens PARATYPES from Shiel sample 792. 480. ephippium; 481. frontal view of instar-II male, showing rostrum and long terminal setae on antennal branches; 482. posterior-ventral region of shell of instar-II male, showing ventral setae and posterior setules unseparated by any denticle; 483. trunklimb I of instar-II male (LS, lateral seta; ODL2, long, feathered lesser ODL seta; CBS', anlage of copulatory brush seta; MS', anlage of male seta on IDL); 484. antennules of instar-II male; 485. antennule of mature male (note long and brushy male seta, M, and far distal origin of antennular seta, AS; aesthetascs are relatively short); 486, 487, postabdomen and postabdominal claws of instar-II male (long, slender and relatively straight basal spines are noteworthy); 488. postabdomen of mature male.

strong keel behind pores; cannot be spread flat without generating excessive folding; narrowed posteriorly and somewhat truncate in lateral view where it meets keel of shell (Fig.435). Rostrum rather short and broad (Fig.439), tapered to a bubble-like tip (Fig.440). IP distance about 60 µm (n=10); PP distance averages 12.6 times IP distance. Eye slightly larger than ocellus, but both small relative to size of animal and close together; distance from ocellus to tip of rostrum many times greater than distance between eye and ocellus; both placed some distance from margin.

*Antennule*. Elongate; antennular seta almost as long as antennule, arising about one quarter from tip; 9 aesthetascs, about one third length of antennule; rounded expansion at base projecting backward.

*Antenna* (Figs 453, 484). Formula: 0(1)-0-3(1)/1-1-3(1). Eight long swimming setae; seta arising from basal segment of endopodite more than half as long as other seven; terminal spines long, about as long as segments from which they arise; spine from basal segment of exopodite well developed; rows of spinules on all segments of both rami and on basal segment (Fig.484).

*Labrum* (Figs 445-452). Anterior margin evenly curved to narrow tip, usually with slight concavity just before tip; posterior margin concave, usually irregularly so; posterior angle rather narrow, considerably less than 90°.

*Trunklimb I* (Figs 437, 438). ODL with 2 setae, smaller one as long as basal segment of longer seta, with many setules arising from distal segment, giving it a brush-like appearance; longer seta with no setules visible with 40x phase objective. IDL with 3 setae, shortest stout to tip and apparently without setules, about as long as basal segment of the other 2; these have rows of long setae anteriorly along distal segment. Middle and posterior setae of middle group of corm setae almost equally long, middle seta slightly longer; well developed feathered and delicate lateral seta arising near base of ODL-IDL ridge (Fig.403).

*Trunklimbs II-V* (Fig.458). Setae in gnathobasic filter combs number 8, 8, 6 and 4 on limbs II-V, respectively; 7, 7 and 4 soft setae on limbs III-V, respectively. Otherwise morphology typical of *Pleuroxus* group. All scraping spines of limb II with fine spinules along distal segment.

*Postabdomen* (Figs 441-442, 472-474). Anal groove strongly concave; preanal angle well developed, somewhat rounded; postanal angle less strong and broadly rounded. Anal groove shorter than preanal portion, which in turn is slightly shorter than postanal; latter tapers distally to rounded distal angle. About 20 marginal denticles or denticle positions; denticles very long, slender, slightly curved; distal denticles single, tightly packed together at bases; proximal denticles with varying number of subdenticles and setae associated; anal groove with 6-7 sequential rows of setae projecting beyond margin. Preanal portion single in distal quarter, with about 4 or 5 transverse ridges, which show up as scallops from side; expands somewhat from side to side proximally. Lateral surface with 2 rows of spinular crescents along postanal portion and along distal part of anal groove; complex arrangement of very many rows of crescents in anterior two thirds of anal groove and in preanal portion. Abdominal setae rather short, barely reach anal groove when extended. Ventral margin long and with distinct break in curvature about one third from proximal end, producing a pronounced bowing outward; 2 angular rows (or crescents) of fine spinules across ventral margin.

*Postabdominal claw* (Figs 441, 442, 474). Long, slender; evenly but weakly curved to bluntish point at tip; concave margin provided with 2 sequential rows of setules, proximal row with longer ones; median surface with row of setules toward convex margin, which project beyond margin irregularly. Two long basal spines, longer one slender, considerably longer than basal width of claw; shorter one even more slender, straight, length about equal to basal width of claw.

**Ephippial female** (Figs 436, 475, 480). Two resting eggs in all ephippial females (Fig.436) and ephippia. Lining of broodpouch heavily pigmented, and pigmentation also in ephippial part of shell, sometimes so heavy it obscures all details beneath. Slough line sharply evident, beginning just posterior to mandibular articulation and then proceeding ventrally and posteriorly toward posterior-ventral angle; junction between ephippium and ventral margin of shell so broad that shell flaps seldom slough off completely (Fig.480). Dorsal margin heavily chitinised within keel. Surface of ephippium with angular tubercles of different sizes.

**Male.** Males show the 3-instar ontogeny characteristic of all chydorids known to date. These include shortening and rounding of the rostrum; thickening of the antennule, development of a long male seta, and often with more than 9 aesthetascs, which are difficult to count; development of copulatory hook, copulatory brush, copulatory brush seta, and male seta on trunklimb I; and often in changes in shape and armament of the postabdomen and the postabdominal claw. All three instars have much the same shape as females - thin, highly arched, almost circular from the side, and with no posterior-dorsal and posterior-ventral angles (break in curvature) on shell.

*Instar-I* (Figs 460, 462). Copulatory hook peg-like; no anlagen of any other setae. Postanal portion of postabdomen shortened, so that all 3 zones subequal in length; stout setae along anal groove where rows of setae develop in instars II and III, and greatly reduced number and development of spinules laterally as compared with female. Genital pore small, located near ventral margin at distance equal to half length of claw.

*Instar-II* (Figs 438, 443, 453, 454, 459, 461, 463, 464, 476, 481-484, 486, 487). Copulatory hook angular and J-shaped (Figs 443, 461, 483). Anlage of male seta on antennule short, stout, weakly divided into 2 segments, arising one third from end of antennule (Fig.459); antennular seta long and slender arising about one third from end. Anlagen of male seta on IDL and of copulatory brush seta. Rostrum shorter and broader than

in female (compare Figs 469 and 481), and although bluntly pointed has 2 small denticles at tip (Figs 453, 454). Postabdomen similar to female in general shape, proportions, and armament, except that ventral margin more strongly expanded basally (Figs 463, 464); marginal denticles nearly all single and with few complications from accessory denticles or spinules; genital pore slightly farther distally than in instar-I and usually with a thin sperm duct coming to it. Postabdominal claw same as in female.

*Mature* (Figs 444, 455-457, 465-467, 477-479, 485, 488). Copulatory hook long, slender, U-shaped, with 3 crescentic ridges crosswise near tip. Male seta on antennule almost as long as antennule, strongly plumose in distal segment (Fig.485); number of aesthetascs indistinct, but seemingly fewer than 12 and possibly only 10. On trunklimb I male seta long and curving forward; copulatory brush a small discrete group of long setae; copulatory brush seta large, elongated, distal segment thin and mostly obscured by copulatory brush. Rostrum short, broad, truncate and weakly rounded at tip, provided with a globular tubercle that is distinctly emarginate, arising subterminally from underside (Figs 455-457); dorsal surface sunken dish-like, so that margin distinctly higher than centre. Postabdomen more elongate and more slender than in instar-II male or female and with a suppressed postanal angle (Figs 465-467, 477-479); crescents and rows of spinules laterally have about same arrangement as in female, but marginal denticles nearly all multiple and arranged in transverse or oblique clusters; genital pore located far distally near base of peduncle for claw (Figs 478, 479); distinct angle at distal end of peduncle ventrally. Postabdominal claw somewhat shorter, stouter, and seemingly slightly more curved than in female. On shell anterior to midventral bulge shell margin rolled inward, and marginal seta, therefore, turned inward; many very slender and long setae here arise from turned-in margin and project ventrally, producing a brushy appearance (Fig.444).

**Length.** Females: overall 0.81-1.75 mm (n=45); first eggs at 1.21 mm; ephippial 1.35-1.68 mm (n=14). Males: instar-I 0.75-0.86 mm (n=12); instar-II 0.82-0.97 mm (n=20); mature 0.93-1.10 (n=20).

## Artificial Key to Populations of *Pleuroxus* and *Pleuroxus*-like Taxa Known from Australia and New Zealand as Treated in this Paper

*Pleuroxus aduncus*, which is redescribed in this paper, is not included in the key, because it does not occur in Australia. *Pleuroxus laevis* Sars, *Pleuroxus denticulatus* Birge and *Pleuroxus similis* Vavra likewise are not included, nor are the six taxa described by Smith and Henry from the region of Sydney. The latter will be considered in a subsequent chapter. It is certain that more, possibly many more, species of *Pleuroxus* and related genera will be distinguished, particularly in Western Australia, as the weakly saline, minute, and ephemeral waterbodies are studied more closely.

1. Shell and head covered with small rounded tubercles ..... 2

—— Shell and head without rounded tubercles ..... 4

2. Setae in gnathobasic filter combs on trunklimbs II-V number 8, 8, 6 and 4, respectively; no sharp keel on head behind pores and on shell; about 20 postabdominal denticles, distal ones almost touching at their bases ..... *Pleuroxus helvenacus* n.sp.

**Note**: This taxon is known only from New Zealand. It has an average of 118 ventral setae on the shell, including the 10 or so at anterior end that arise submarginally and project centrally, rather than outward. Labrum long and narrow. Single small rounded denticle (range 0-2) at posterior-ventral angle of shell. PP distance averages 5.4 times IP distance.

—— Setae in gnathobasic filter combs on trunklimbs II-V number 10, 10, 7 and 5, respectively; sharp keel dorsally behind posterior headpore; about 12-15 postabdominal denticles ..... *Plurispina* n.gen. – 3

3. Preanal portion of postabdomen much shorter than anal portion, which is about equal to postanal portion; tip of rostrum weakly bifid; tubercles on shell moderately dense ..... *Plurispina chauliodus* n.sp.

**Note**: The male of this taxon is highly distinctive; with 2 strong, tusk-like denticles arising submarginally from tip of rostrum, and with the distal segment of the male seta on the antennule strongly brush-like. Shorter seta on ODL also strongly brush-like. About 107 ventral setae on shell. PP/IP ratio about 7.6. Spines on claw very short, longer spine less than width of claw.

—— Preanal portion of postabdomen about equal in length to anal portion, and both much shorter than postanal portion; tip of rostrum beadlike; tubercles on shell larger and densely packed, producing a general opacity ..... *Plurispina multituberculata* n.sp.

**Note**: Entire shell covered with radiating ridges and deep troughs separating them; no actual striae on shell, these being approximated by rows of tubercles. Shorter seta on ODL without brush-like setation. About 122 ventral setae on shell. PP/IP ratio 6.8.

4. Length of anal portion less than that of preanal and postanal; 2 resting eggs ..... 5

—— Length of anal portion about equal to preanal, and both less than postanal; 1 resting egg ..... 6

5. About 90 setae on shell; PP/IP ratio about 4.7; polyembryonic ..... *Archepleuroxus baylyi* Smirnov & Timms

**Note**: In addition, *Archepleuroxus* has about 12 denticles on the postabdomen, usually no tooth on the shell although occasionally one very small tooth. The postabdominal claw of the male is shorter than in the female and is somewhat sigmoid.

—— About 180 seta on shell; PP/IP ratio about 12.6; only 2 parthenogenetic eggs ..... *Planicirclus alticarinatus* n.gen., n.sp.

**Note**: This is by far the largest species of the group, and the largest chydorid known outside the two genera *Eurycercus* and *Saycia*. It reaches a length at least up to 1.75 mm. The species is almost circular in shape and strongly flattened. It has a very sharp keel on the shell, the latter being covered with radiating ridges. No tooth is present. The postabdomen has about 20 marginal denticles, closely packed distally, and has many crescents of setules laterally in the anal and preanal portion. The middle and posterior setae of the middle group of corm setae are almost equally long. The distal segment of the male seta on the antennule is strongly brush-like.

6. Surface of shell and head behind pores covered with small dimples; about 100 ventral setae on shell; PP/IP ratio mostly about 6; strong tendency toward 9 setae in gnathobasic filter comb of trunklimb III ..... *Pleuroxus foveatus* n.sp.

**Note**: The shell is weakly ridged, there is a small triangular tooth on the shell, and the preanal and anal portions of the postabdomen, which are roughly equal in length, are much shorter than the postanal portion. The shell flaps of the ephippium are only narrowly attached posteriorly, and hence can easily be sloughed off after molting.

—— Surface of shell smooth, without dimples; mostly fewer than 90 ventral setae on shell; PP/IP ratio less than 4; 8 setae in gnathobasic filter comb of trunklimb III ..... 7

7. Eight to 10 marginal denticles, all multiple; distinct, sharply pointed tooth on shell ..... *Pleuroxus hastirostris* Sars

**Note**: This taxon is from New Zealand. It has 80 or fewer ventral setae on the shell, a PP/IP ratio of less than 3, and the male has 9 transverse rows of the same size setae on the postabdomen, none in any rows sufficiently larger than the others to be considered a denticle.

—— Twelve to 13 marginal denticles, distal ones simple; no tooth on shell or else a very small one ..... *Pleuroxus inermis* Sars

**Note**: This is the commonest species of *Pleuroxus* in southern Australia. It is well defined by the various characters used in the key.

## Other Taxa

Besides the nine taxa considered in detail in this paper, Table 1 lists three taxa described from other continents, a taxon described by Smith (1909) from Tasmania, and five by Henry (1918, 1922) from New South Wales. The six taxa from Australia were judged to be possible members of the *Pleuroxus* group, either because of the generic name used by the describers or because of their morphology. The latter in all instances is inadequately described and illustrated for our present needs. An attempt was made without success to locate specimens of Smith's taxon, but type specimens of all of Henry's taxa except *Pleuroxus reticulatus* were borrowed from the Australian Museum. In addition, three specimens from Australia labelled *Pleuroxus aduncus* and three labelled *Pleuroxus denticulatus* were borrowed.

The three specimens labelled *Pleuroxus aduncus* are probably *P. inermis* instead. The three specimens labelled *Pleuroxus denticulatus* are not all from the same taxon: one resembles Henry's *Pleuroxus australis*, the other two have a *Pleuroxus laevis*-type postabdomen, and none of them is Birge's *Pleuroxus denticulatus*. No specimens of *Alonella nasuta* were available, and hence the taxon could not be evaluated properly. *Pleuroxus reticulatus* belongs in two other genera. *Chydorus denticulatus* seems quite certainly to be *Pleuroxus inermis*. The holotypes of Henry's *Pleuroxus australis*, *Chydorus unispinus* and *Chydorus jugosus* are all properly in *Pleuroxus*, but insufficient evidence can be discerned to determine, especially for *Chydorus jugosus*, to which taxa they correspond. In addition to *Alonella nasuta*, Henry's species must therefore be *nomina dubia* at present. This illustrates strikingly the insufficiency of single specimens to characterise a taxon. Populations containing diverse instars and stages must be available for a reasonable understanding.

1. *Pleuroxus aduncus* (Jurine, 1820). This taxon described from France is now known not to occur in Australia. Three specimens collected by B.V. Timms and so labelled are in the AM. All specimens are mounted in a medium with poor refractive index for resolving fine details.

a. *Slide P34983*. Mount House Station, Kimberleys, 4 Oct. 1982. (BVT?). Parthenogenetic female without eggs, length 0.51 mm. Body quite high, tapered downward posteriorly to a posterior-dorsal angle that is distinct; posterior-ventral angle more rounded, contains a small tooth on one side only. About 77 ventral setae on shell,

excluding any internal setae at anterior end. Ventral portions of about 9 curved striae visible in anterior part of shell. Ocellus and eye about equal in diameter. Rostrum short. Labrum rather short and broad, tip narrowly rounded. IP distance 56 µm, PP 189 µm, PP/IP ratio 3.4. Postabdomen: anal region = preanal which is less than postanal; broad, tapered distally and rounded somewhat at end; denticles cannot be counted, and lateral crescents not visible. Other details not visible.

This specimen is probably *Pleuroxus inermis* Sars, 1896.

b. *Slide P34985*. Richmond, Qld, 10 July 1984. BVT. Parthenogenetic female with 2 early embryos, length 0.48 mm. Body reasonably high, sloping down to short posterior margin, with a slight concavity just before posterior-dorsal angle. Posterior-ventral angle narrowly rounded, and with 1 small but distinct tooth at change in curvature. Postabdomen: preanal portion less than or equal to anal which is less than postanal; armature visible only vaguely - possibly 10-12 long, slender denticles. Both basal spines of claw long, longer one slender and curved away from claw, smaller one straight and slender, both equal to or slightly greater than basal width of claw. Eye slightly larger than ocellus. Headpores not visible. Other details obscure.

This specimen is probably *Pleuroxus inermis* Sars, 1896

c. *Slide P34984*. Palm Valley, NT, 25 June 1981. BVT. Parthenogenetic female with 2 early embryos, length 0.49 mm. Poor resolution from mounting medium, so that most details only vaguely perceivable at best. Seems to share many of the details of the previous specimen, although anal groove is relatively longer, and there are 2 teeth on 1 valve, one on the other. The shape of the animal is much the same as for the 2 previous specimens, with a rather short rostrum and reasonably distinct posterior-dorsal and posterior-ventral angles.

This specimen is possibly *Pleuroxus inermis* Sars, 1896.

None of these specimens is *Pleuroxus aduncus* (Jurine, 1820), and with the scarcity of details it is quite impossible to tell what they are. They are most closely related to *Pleuroxus inermis*, as defined in the present study, but the rostrum is somewhat shorter, the labrum more broadly expanded, and the count of ventral setae on the shell smaller than is characteristic of *P. inermis*. Possibly they represent an undescribed species.

2. *Pleuroxus denticulatus* Birge, 1879. The three specimens so labelled in the AM were also collected and mounted by B.V. Timms. Although no taxa in the *Pleuroxus laevis* group or *Pleuroxus denticulatus*-group were treated in this paper, the specimens were examined cursorially.

a. *Slide P27722*. Keil's Dam via Macksville, NSW, 24 Aug. 1967. (BVT?). Parthenogenetic female with 2 advanced embryos, length 0.39 mm. Rather elongate and not overly high; both posterior-dorsal and posterior-ventral angles distinct; 2 broad-based triangular teeth on each valve; only 64 ventral setae on shell, not counting any interior setae at anterior end, which were not visible. IP distance 54 µm, PP 124 µm, PP/IP ratio 2.3. Postabdomen: anal region less than preanal which is much less than postanal; general shape somewhat similar to *Pleuroxus denticulatus*: both dorsal and ventral margins straight, tapering distally to acutely truncate distal end; possibly 12 or 13 denticles, rather stout, all single distally but proximal ones with short rows of setae proximally. Postabdominal claw long, slender; basal spines quite straight, longer one a little longer than basal width of claw, shorter one less than half as long. Specimen mounted in balsam, but obscured by being at edge of coverglass.

This specimen definitely is not the same as Birge's *P. denticulatus*. It resembles *Pleuroxus australis* in the general shape of the postabdomen and in the nature of the teeth on the valves.

b. *Slide P34988*. Mataranka, NT, 13 July 1981. BVT. Parthenogenetic female without embryos, length 0.40 mm. Body quite low, and dorsal margin slightly concave before posterior-dorsal angle, as in *P. aduncus*. Posterior-ventral angle well formed, with 3 broad-based, pointed teeth on each valve; 76 ventral setae, not counting any interior setae forward. Rostrum long, slender, bent posteriorly and tucked against body. Eye larger than ocellus. Postabdomen similar to that of *P. laevis* in shape: anal portion less than preanal which is much less than postanal; about 12 marginal denticles, all single, straight, slender, and well separated from one another. Postabdominal claw with longer basal spine straight and considerably longer than basal width of claw, shorter one much less than half as long. Other details obscure.

c. *Slide P34989*. Kaban, Qld, 18 July 1983. BVT. Parthenogenetic female with 2 embryos, length 0.43 mm. Ventral margin convex; dorsal margin high but bending down sharply to indistinct posterior-dorsal angle; posterior-ventral angle about 90°, narrowly rounded, with 3 broad-based and pointed teeth at lower edge of posterior margin; ventral setae 79, not counting any anterior setae, which were not visible; no curved striae visible on shell anteriorly and no shell markings. Eye almost twice size of ocellus. IP distance 61 µm, PP 142 µm, PP/IP ratio 2.3. Postabdomen of *P. laevis* type: anal region less than preanal which is much less than postanal; ventral margin gently and evenly convex; dorsal margin essentially straight, or even a little concave, provided with about 12 short, slender, pointed, well-separated denticles, only a couple of the proximalmost ones not being single. Postabdominal claw slender; longer basal spine slender and curved outward, considerably longer than basal width of claw; smaller one very slender, less than half as long as longer ones. Other details obscure.

None of these three specimens is any of the nine species considered in detail in this paper, and none of them is *P. denticulatus* Birge. Moreover, it seems quite certain that they are not all from the same taxon. As it is impossible to describe a species from a single specimen, even when details are clear, identification will have to wait until large populations containing males and ephippial females become available.

3. *Alonella nasuta* Smith, 1909: 84, pl.16, figs 4,5.

No specimens could be located in the AM or in the Hope Collections at Oxford University, the latter of which contains specimens of some of the other taxa Smith described in this paper. Hence the following comments are based entirely on Smith's description.

The illustration suggests this taxon might belong to the *Pleuroxus* group. The animal has a long, bluntly-tipped rostrum, and the carapace has a series of radiating striae (or ridges) everywhere except in the anterior-dorsal region. The carapace is described as 'regularly oval without any marked angles', although the figure shows a change in curvature posteriorly, which is probably the posterior-dorsal angle. The postabdomen is *Pleuroxus* in shape, with four 'stout short spines' distally along the postanal margin and five 'groups of bristles' anterior to these. The length is given as 0.5 mm, which puts this among the smaller *Pleuroxus* taxa. Smirnov & Timms (1983) list this taxon as a synonym of *P. aduncus*, which is unrealistic because of the markings on the carapace, the lack of any teeth at the posterior-ventral angle, and the single distal denticles on the postabdomen.

The taxon at present must be considered a *nomen dubium.*

4. *Pleuroxus reticulatus* Henry, 1918: 478-479, pl.42, figs 13,14. The taxon illustrated here is a species of *Alonella*, most likely *A. clathratula*, but the specimen deposited as the holotype and the taxon illustrated in Henry (1922) are considered to be in a new genus by Smirnov, listed as *Monoporus* in Smirnov (1977) but changed to *Monope* by Smirnov & Timms (1983), the name of the taxon now being *Monope reticulata* (Henry, 1922). The 1918 description is of the *Alonella* taxon. It is much smaller than *Pleuroxus* or *Monope*, being listed as only 0.31 mm.

5. *Chydorus denticulatus* Henry, 1918: 480-481, pl.42, figs 15,16. Slide P4334 = HOLOTYPE. Parthenogenetic female with 2 eggs, length 0.60 mm. Body highly arched, with quite a distinct posterior-ventral angle and less distinct posterior-dorsal angle; each valve has a small tooth at posterior-ventral angle; 8 or 9 curved striae anteriorly, which bend posteriorly at bottom and join a stria continuing posteriorly close to ventral margin; no other shell markings apparent; 92 ventral setae on left side, including about 8 submarginal setae at anterior end, and 83 on right side, not including any of these anterior setae; no keel. Rostrum quite short. IP distance 54 µm, PP 224 µm, PP/IP ratio 4.1. Terminal spines on antenna very short; any spine present on basal segment of exopodite obscured by debris. Postabdomen: anal region less than preanal which is less than or equal to postanal; 13 postanal denticles, all multiple except for a few of the distalmost ones. Postabdominal claw with 2 basal spines, longer of which is considerably longer than basal width of claw, slender, and curved away from claw. According to Henry, the carapace is marked by small pits, which become larger and more conspicuous dorsally. Henry also states that there are 16 groups of spines along the postanal margin of the postabdomen and that the length of the taxon is 0.46 mm. These are seemingly minor discrepancies for the specimen examined. Smirnov & Timms (1983) list this taxon as a synonymy of *Pleuroxus aduncus*. Instead it is quite certainly *Pleuroxus inermis* Sars, 1896.

6. *Pleuroxus australis* Henry, 1922: 45, pl.7, fig.3. Slide P5893 = HOLOTYPE. Parthenogenetic female without embryos, length 0.45 mm. Body rather low, not expanded dorsally; no keel; suggestions of dimples on shell, but otherwise no markings visible except about 10 curved striae anteriorly; 78 ventral setae on left valve, 75 on right, neither count including any anterior setae; 3 teeth on left valve, 2 on right, broad-based and pointed, deployed along lower posterior margin as in *P. aduncus*; posterior-dorsal angle weak, posterior-ventral angle strong, emphasised by teeth; eye twice as large as ocellus; IP distance 63 µm, PP 187 µm, PP/IP ratio 3.0. Postabdomen: mostly obscured by detritus so that shape and relative length of zones not visible; seems elongate; acutely truncate at end, and with only 1 strong denticle here; the couple other more proximal denticles visible are smaller. Postabdominal claw rather stout; longer basal spine much longer than basal width of claw, shorter one less than half as long.

This taxon is not related to any considered in this study. Smirnov & Timms (1983) list it as a synonym of *Pleuroxus similis*, which does not seem correct from the details observable, besides which *P. similis* was described from Chile and hence seems unlikely to be in Australia. At present *P. australis* must be considered a nomen dubium.

7. *Chydorus unispinus* Henry, 1922: 46, pl.7, figs 4,4a. Slide P5892 = HOLOTYPE. Parthenogenetic female with 2 large eggs, length 0.63 mm. Highly arched dorsally; both posterior-dorsal and posterior-ventral angles reduced by curvature; single, small, slender tooth on either side before posterior-ventral angle; no keel; 8 curved striae anteriorly, continuing posteriorly as a stria closely parallel to ventral margin; no other shell markings; 72 ventral setae on right side, excluding any setae along anterior margin. Eye half again to almost twice as large as ocellus. IP distance 62 µm, PP 171 µm, PP/IP ratio 2.8. Antennules rather short and broad; antennular seta arises about two fifths from end; aesthetasc field surrounded by triangular projections. Postabdomen: anal region equals preanal which is less than postanal; wide, slightly flared out basally; 13 or 14 postanal denticle positions; distal denticles mostly single, proximal ones each with a row of accessory setules. Basal spines on postabdominal claw rather short; longer one about equal to basal width of claw, possibly a little longer; shorter one only about half basal width.

This specimen cannot be associated for certain with any of the taxa considered in this paper. It has a small PP/IP ratio and a small number of ventral setae. The postabdomen and claw resemble those of *Archepleuroxus*, except that there are no chevron-like folds across the distal preanal margin, and the anal portion is not distinctly shorter than the preanal. If this were *Archepleuroxus* it would be from near the bottom of the reproductive size range and hence easily could

have just two eggs. The teeth on the shell, though, are not at all like *Archepleuroxus*. The specimen also resembles *Pleuroxus inermis* in many respects. Except for the prominent shell tooth and the very small number of ventral setae, it resembles the South Australian population of *P. inermis*, F7961. Henry likened this taxon to *Chydorus* (= *Ephemeroporus*) *barroisi* group because of the slender, backwardly directed tooth at the posterior-ventral angle. However, the large labrum has no teeth, the postabdomen is very different in structure from *Ephemeroporus* species, and two separated median headpores are readily visible. Smirnov & Timms (1983) consider it a synonym of *Pleuroxus aduncus*, which from the redescription in this paper is obviously incorrect. *Chydorus unispinus* is a member of the *Pleuroxus* group of species, but for the moment it must be considered a *nomen dubium*.

8. *Chydorus jugosus* Henry, 1922: 46, pl.7, figs 5,5a. Slide P5889 = HOLOTYPE. This is the taxon that initiated this paper. For a while I labelled nearly everything from Australia as *Pleuroxus* cf. *jugosus*, not knowing to which of the many taxa Henry's *jugosus* corresponded. A close study of this specimen, however, did not reveal enough positive characters to make a firm decision, and hence this taxon, at least for the present, must be regarded as a *nomen dubium*. Henry gives the size of the taxon as 0.74 mm, but this specimen measures only 0.56 mm. Comparison with two possibly related taxa from Western Australia - *Plurispina chauliodus* and *Plurispina multituberculata* - puts the specimen near the upper size limit of instar-I, although its morphology, especially of the postabdomen, indicates that it is an instar-II individual.

A single specimen, especially a juvenile, is insufficient to characterise a taxon. The specimen has tubercles on its shell, as do the two species of *Plurispina* from Australia plus *Pleuroxus helvenacus* from New Zealand, but too few details of morphology can be resolved to determine what its affinities are. If it has a greater than normal number of setae in the gnathobasic filter combs of trunklimbs II-V, then it certainly is a member of the genus *Plurispina*. Until more specimens become available, though, the taxon should be left in *Pleuroxus*, which is certainly more appropriate than *Chydorus*. This inadequate holotype of *Pleuroxus jugosus* of Henry is described here in greater detail to help characterise the taxon and to assist in its identification when more individuals become available.

### *Pleuroxus jugosus* (Henry)

Figs 489-493

*Chydorus jugosus* Henry, 1922: 46, pl.76, figs 5,5a.
*Pleuroxus jugosus*.–Smirnov & Timms, 1983: 22-24, figs 21, 22 (not *Chydorus jugosus* Henry, 1922). [Note: Most of the description and all illustrations in this paper are for *Plurispina chauliodus* n.sp.]

**Description of immature holotype female** (Figs 489-491). Rostrum of this specimen distorted, bent forward. Eye and ocellus in unnatural positions from contraction of tissues away from headshield; ocellus almost as large as eye. Apparently a keel on head behind pores and on shell; IP distance 45 µm and PP distance 149 µm, thus giving a PP/IP ratio of 3.3, which is considerably less than in the tuberculated species that are possibly related. Diagonal ridges and grooves on shell, anterior ones indicated by rows of fine tubercles (Fig.491), posterior ones more prominent, indicated in drawing by dashed lines (Fig.489). Entire head and shell covered by rather coarsely scattered fine tubercles. Colour somewhat darkish, but everything clear in mounted specimen. Posterior margin short, weakly convex; both posterior-dorsal and posterior-ventral angles rounded; no tooth on shell; ventral margin evenly convex. Aesthetascs stop way short of tip of rostrum. Rami of antennae short and stout; terminal spines less than length of terminal segments. Keel of labrum rather short, broadly rounded at tip; posterior angle roughly 90°. Postabdomen with preanal portion shorter than anal portion, which in turn is considerably shorter than postanal portion (Fig.490); about 13 denticles in postanal portion, distal ones being simple, but proximal ones have smaller accessory denticles or setae arranged proximal to them; course of denticles not parallel, distal ones pointing proximally, proximal ones distally, and central ones at right angles; scallops of setae or spinules on lateral surface not visible, nor are crescents of spinules across ventral margin. Postabdominal claw with a marked bend in curvature in concave margin; both basal spines very long and slender, longer than basal width of claw; preanal angle of postabdomen subdued, and postanal angle broadly rounded. Ventral setae on shell 89 on left side and 92 on right side, in both instances excluding any submarginal setae arising anteriorly, which are not visible. Other species have about ten such setae.

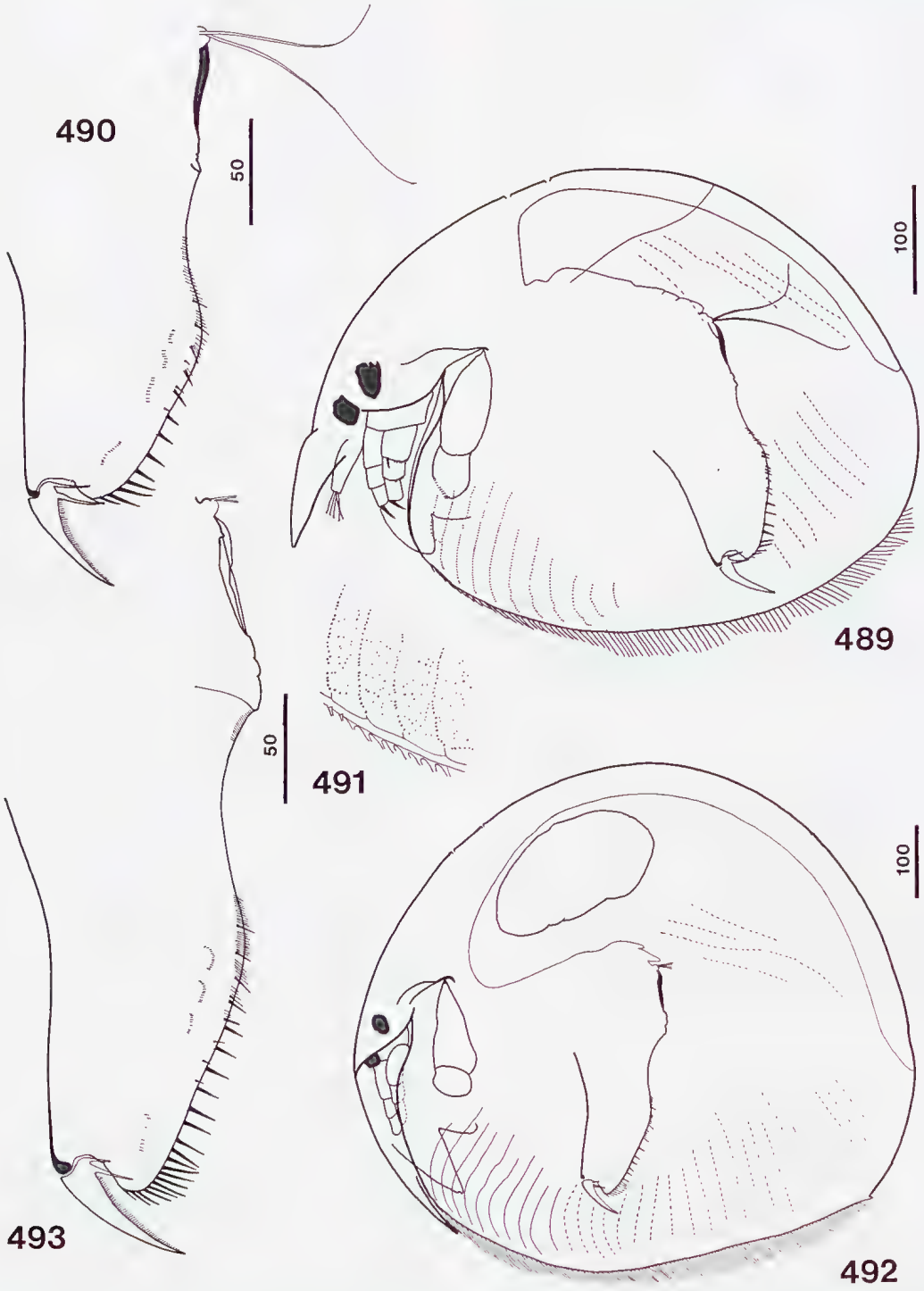
Figures 492 and 493 are drawn from the specimen that Smirnov deposited in the AM as *Pleuroxus jugosus* to help bolster the description of the taxon, his number 2805 and the Museum number P27723. Unfortunately, this specimen is from the taxon *Plurispina chauliodus*, which has many distinctive characters as revealed in the species description. The immature holotype is still the only extant specimen of *Pleuroxus jugosus* (Henry, 1922).

**Remarks.** This taxon has fine tubercles on the shell and head, probably a keel, and the preanal portion of the postabdomen is shorter than the anal portion. Moreover, there are about 100 ventral setae on the shell, and the postabdominal denticles extend in different directions rather than being roughly parallel. All these characters apply in varying degrees to the two species of *Plurispina* from Western Australia and to a lesser extent to *Pleuroxus helvenacus* from New Zealand. The elongate body, though, and the short PP distance may be reflections of immaturity rather than being characteristic of adult specimens. The taxon seems

related to the two tuberculate species from Western Australia, but counts of the number of spines in the gnathobasic filter combs are needed to determine if it is a member of the genus *Plurispina*.

## Discussion

The high diversity of the chydorid fauna of Australia was suggested by the paper of Smirnov & Timms (1983). Smirnov in this paper and in his previous papers (Smirnov, 1971, 1977) described five new genera, 14 new species, and two new subspecies of chydorids from Australia. In this paper, considering just the genus *Pleuroxus*, I have described two new genera and five new species. Two of the species – *Pleuroxus inermis* and *Pleuroxus foveatus* – each possibly represents more than one species, but the material available is not adequate to decide. *Pleuroxus hastirostris* and *P. inermis*




**Figs 489-493.** *Pleuroxus jugosus* (Henry, 1922) HOLOTYPE, specimen P5589, from AM, immature female: 489. side view; 490. postabdomen; 491. arrangement of denticles into striae in anterior-ventral part of shell. *Plurispina chauliodus* n.sp., specimen P27723, AM, erroneously labelled *Pleuroxus jugosus* by Smirnov & Timms (1983); 492. side view of mature parthenogenetic female; 493. postabdomen.

closely resemble in general characters species of *Pleuroxus* that occur in the Northern Hemisphere. The other six species resemble *Pleuroxus* in many respects, but differ sufficiently so that four of them are removed to new genera, including *Archepleuroxus* established by Smirnov & Timms. The two remaining species are retained in *Pleuroxus*. *Pleuroxus foveatus* might well be placed in a different genus, although its differences from traditional *Pleuroxus* species are not so great as in the others. A decision about *P. helvenacus* cannot be made at the moment, because no gamogenetic individuals are available. Although it has tubercles on the shell and head, it is markedly different from the other two species that share this character and does not belong in the genus established for them.

This fauna was difficult to work with, first because nearly every population studied was suspected initially to be a new species, and second because at first none of the taxa stood out clearly from the others. However, a careful tabulation of the characters found to be important (Table 2) revealed quite clearly the major taxa present. The characters that were most useful in defining the species are: 1) size (length); 2) size-frequency distribution by instars and stages (Fig.1); 3) number of ventral setae on the shell; 4) surface markings or patterning on the shell and head; 5) presence or absence of a shell tooth and its characteristics; 6) whether the dorsal surface transversely was rounded, ridged or keeled; 7) amount and pattern of pigmentation in intact animals and their ephippia; 8) the PP/IP ratio; 9) nature of the rostrum in males and females; 10) size and feathering of the smaller ODL seta; 11) which of the corm setae is the longest; 12) the number of setae in the gnathobasic filter combs of trunklimbs II-V; 13) number, nature and orientation of the postabdominal denticles; 14) relative length of the preanal, anal and postanal portions of the postabdomen; 15) relative length of the basal spines on the claw; 16) size and shape of the claw of the mature male; 17) whether or not the male seta on the antennule is brush-like; 18) whether the shell flaps are narrowly or broadly attached to the ephippium posteriorly; 19) two or many parthenogenetic eggs per instar, and 20) one or two resting eggs per ephippium.

Other characters used are apparent from the descriptions, but these are more difficult to quantify. Counts of ventral setae were used earlier by Frey (1976) to separate *Pleuroxus pigroides* from other species of the genus in northern Europe, but this is the first time counts of the setae have been used to help separate members of a group of broadly related species. As mentioned in the species write ups, the number of setae per taxon remains roughly constant over all stages and all instars after instar-I. The number of setae in the gnathobasic filter combs, the relative length of the three portions of the postabdomen, and the PP/IP ratio of mature parthenogenetic females are being used for the first time. Together these characters provide a sensitive means for distinguishing the various species and genera.

There are several points of interest raised by this material. First, all taxa considered are restricted to Australia or New Zealand. Neither of the two species in New Zealand occurs in Australia. The European species *Pleuroxus aduncus* was claimed to occur in Australia, but it does not. What this suggests is that the chydorid Anomopoda in Australia, as well as various groups of plants and animals that have already been studied, have been isolated from the rest of the world for 60 million years or so, since the time that Australia separated from the last remaining bit of Gondwana. This period of time was sufficient for the differentiation of many new taxa now confined to Australia. The restricted occurrence of these taxa and the fact that, at least for *Pleuroxus* and related genera, no taxa that have evolved outside of Australia have invaded the continent over this long period, indicate that passive distribution of resting eggs by wind and birds cannot be accomplished as easily as believed by persons who accept the distribution of the chydorids as cosmopolitan. Studies of morphological differences between populations having the same name on different continents have shown the taxa to be different at the species level (see Frey, 1986 for a partial review). Such comparisons have been made between cognate populations in North America, Europe, South-east Asia, Australia, South America, and Sri Lanka. They indicate that one should be cautious about accepting as valid for any chydorid a name originating on some other continent. Only in the Tropics and Subtropics does there seem to be any possibility for conspecific populations to occur naturally on different continents (Rajapaksa & Fernando, 1982, 1987).

Second, the situation in Australia is even more complicated than this, because closely related species can occur in the same region. Australia has had a complicated geological history over the past 60 million years, with at one time the continent being separated into eastern and western portions by the sea. Separation evidently was long enough for many of the isolated populations to differentiate into new species, and there undoubtedly have been other interruptions of formerly continuous ranges. What has become apparent is that many of the taxa in Western Australia seem not to occur in the eastern part of the continent. They are associated with special kinds of aquatic habitats - extremely shallow bedrock pools that dry up completely each summer; waterbodies of varying salinity, chiefly sodium and chloride, to which a number of species of *Pleuroxus* and related genera have adapted; larger ponds and lakes that tend to be seasonal and in consequence may experience changes in salinity; and others. Such waterbodies in Western Australia and in other arid or semi-arid parts of the continent, have been barely sampled for Cladocera, chiefly by Bayly and Shiel in Western Australia, Timms in Queensland and New South Wales, Williams and Morton in South Australia, Bayly, Morton, and Shiel in Victoria, and Morton, Shiel, and Timms in Tasmania. The high diversity recovered from limited sampling suggests that other species of *Pleuroxus* and related genera will be revealed by intensive sampling over the year of such special habitats.

Third, there are number of morphological features that are highly distinctive for particular species. For example, the male seta on the antennule of *Plurispina chauliodus* and *Planicirclus alticarinatus* is strongly brush-like in the distal segment, whereas other taxa have this structure without lateral setules. Previously the only chydorids known to have a brush-like seta were *Saycia cooki* (Frey, 1971), and *Pleuroxus scopuliferus* Ekman, 1900. In addition, the lesser ODL seta varies in size, usually being quite short and with either none or with only a few barely distinguishable setules arising from the distal segment. In the same two species mentioned above, however, the seta is considerably longer and it is strongly brush-like in the distal segment. Most of the chydorids other than species of *Eurycercus* and *Saycia* have only a single ephippial egg, but a few species, such as *Chydorus ovalis, Chydorus biovatus,* and possibly *Camptocercus lilljeborgi* have two (Fryer & Frey, 1981), and also *Chydorus piger* (Frey, 1985). Collections of *C. biovatus* from different lakes in Montana have shown this character to be constant for the taxon, as likewise it is for *C. ovalis* and probably also *C. piger*. Thus, the two-egged condition seems unvarying for the taxa that have it. In the present study, two ephippial eggs were found in *Archepleuroxus baylyi* and in *Planicirclus alticarinatus*, thereby increasing the known number of species with two ephippial eggs to six. *Archepleuroxus* is also polyembryonic, the first instance of such a condition in the subfamily Chydorinae. The other instances are the various species in *Eurycercus* and *Saycia* in two other subfamilies.

In my initial examination of the populations selected for study I scarcely knew what to call any taxon. Except for *Pleuroxus hastirostris* and *Archepleuroxus baylyi*, everything else was labelled *Pleuroxus* cf. *jugosus*, a most unsatisfying condition. Not until I began making detailed counts and measurements and arranging the data in tabular form (Table 1) did the various taxa begin to emerge clearly. And in the end, not one of them could be labelled *P. jugosus*! This is the kind of resolution of taxa that I am confident will be repeated, perhaps may times, in Australia, and no doubt will also occur in other parts of the World when their taxa are studied comparatively and in detail. The number of taxa everywhere, even in Western Europe, is greater than presently accepted in the cosmopolitan mode of thinking about the evolution in this group.

## Summary

The *Pleuroxus* species and related taxa described here show wide morphological variation (summarised in Fig.1 and Table 2). *Pleuroxus hastirostris* is slightly the smallest species, and *Planicirclus alticarinatus* by far the largest. The three populations judged to be *Pleuroxus inermis*, including a population raised from mud by G.O. Sars (1896), are all about equal in size and have much the same population structure, even though the Frey 8026 population from Western Australia is smaller stage by stage and instar by instar than the Frey 7961 population from South Australia. The three populations of *Pleuroxus foveatus* are somewhat larger than the *inermis/hastirostris* species. These populations are considered to be the same species, even though there seem to be marked differences in size-structure of instars and stages among the populations. Moreover, nearly all specimens have one more seta in the gnathobasic filter comb of trunklimb III, which suggests possibly a differentiation at the generic level. *Archepleuroxus baylyi* begins at about the same length at the small end but extends to much larger sizes at the large end. The two species of *Plurispina* from Australia and *Pleuroxus helvenacus* from New Zealand extend from about 0.5 to about 0.9 mm, and then *Planicirclus* dwarfs everything else, ranging from 0.75 to 1.75 mm in length. Thus, size distribution alone separates these taxa into at least four and possibly five groups. Although gamogenetic individuals are present in most of the populations studied, unfortunately they are absent from five of them. Hence, the precise characterisation of some of the taxa is difficult to achieve with the present material.

All these taxa except the two species of *Plurispina* have the curved striae on the anterior part of the shell that are considered characteristic of most *Pleuroxus* or *Pleuroxus*-like species. All have the ventral setae on the shell arising from the margin, except for about ten to 15 anteriorly, which arise strongly submarginally along a line that moves inward from the shell margin. In the anterior half of the ventral margin the setae arise from expanded bases, resulting in a weak saw-like configuration. But the number of shell setae varies tremendously, from about 80 in *Pleuroxus hastirostris* to almost 190 in *Planicirclus alticarinatus*. The *Pleuroxus foveatus* populations uniformly have about 100, and the three tuberculate taxa have about 110 to 120 setae. The number of setae per taxon is quite uniform over all instars and stages, being only slightly fewer in instar-I individuals. Except for this one instar, there is no real increase in number during instar ontogeny of either males or females.

Shell markings vary considerably. The small species have smooth shells except for the curved striae in the front. The four populations called *Pleuroxus foveatus* all have small dimples covering the shell. The two species of *Plurispina*, the New Zealand *Pleuroxus helvenacus*, and Henry's single specimens of *Pleuroxus jugosus* are covered with small tubercles at different densities, and in addition they have radiating ridges or folds. *Planicirclus* has the latter to a much greater extent.

The armament at the posterior-ventral corner of the shell is variable. A tooth if present is usually very small, often rounded rather than pointed, and at times easily overlooked. In *Pleuroxus inermis* the specimens from the Sars sample usually had a very small tooth that was difficult to discern because of being oriented along the margin of the shell and not projecting outward. Sars named the taxon *inermis* because it had no tooth, so he thought. The population from South Australia nearly

always had a tooth, whereas the population from Western Australia seldom had one. *Planicirclus* had no tooth on any specimen, and *Archepleuroxus* seldom had a tooth. In contrast, the teeth on *Pleuroxus aduncus* are large, most commonly two in number, and oriented differently than in the Australian taxa.

The small species have the top of the shell rounded from side to side, the others either have a ridge or a keel, with *Planicirclus* having a very sharp and broad keel, which begins on the head immediately behind the pores. The keel on the two species of *Plurispina* likewise begins immediately behind the pores.

The interpore (IP) distance varies only moderately among the taxa, being greatest in *Pleuroxus aduncus*, but the postpore (PP) distance is markedly different, resulting in a PP/IP ratio varying from 2.6 in *Pleuroxus hastirostris* to 12.6 in *Planicirclus*. Aside from *Pleuroxus inermis*, which has a relatively small ratio of three and one half to four, the other taxa range roughly from five to seven.

Typically the species of *Pleuroxus* have 8, 8, 6 and 4 setae in the gnathobasic filter comb of trunklimbs II to V, respectively, but the *Plurispina* species have 10, 10, 7 and 5, and the *Pleuroxus foveatus* populations tend to have 8, 9, 6, and 4, the number on limb III in the Shiel 839 population being either 8 or 9 and a few specimens in the Shiel 857 population having 8 instead of 9 setae here. Since the number of these setae is much the same in all species of the subfamily Chydorinae, a marked and consistent difference indicates a different evolutionary line. *Pleuroxus helvenacus* from New Zealand grossly resembles the two *Plurispina* species in shape and in having rounded tubercles scattered over the shell, but its gnathobasic setae number 8, 8, 6 and 4. In many respects it seems more closely related to *Planicirclus*, particularly in the armament of its postabdomen. All the taxa have 7, 7 and 4 feathered setae on the exopodites of trunklimbs III to V, respectively. On trunklimb I the length and nature of the smaller ODL seta varies from taxon to taxon. In most taxa this seta is short and bare, but *Plurispina chauliodus* and *Planicirclus* are unique in having this seta strongly brush-like.

The relative lengths of the preanal, anal and postanal portions of the postabdomen are highly variable among the species. Most commonly the preanal and anal portions are about equal in length, but in *Pleuroxus helvenacus* the preanal portion is shorter than the anal portion, and in *Plurispina chauliodus* it is much shorter. In *Archepleuroxus* and *Planicirclus* the anal region is the shortest of the three. In all species the postanal region is the longest, or else equal in length to the preanal or anal portions. In the large species the ventral margin of the postabdomen flares out markedly basally, and there is a much more extensive lateral armament of rows and crescents of setae. The number and nature of the postabdominal denticles is also variable, ranging from seven to ten *in P. aduncus* and *P. hastirostris* to about 20 in *Pleuroxus helvenacus* and *Planicirclus*. The denticles also differ as to whether they are single or multiple, most commonly being single distally and multiple proximally. *Pleuroxus aduncus* and *P. hastirostris* have all the denticles multiple. *Pleuroxus helvenacus* and *Planicirclus* have their distal denticles so close together that they are essentially touching at their bases.

All the males proceed through a three-instar ontogeny, which is apparently characteristic of all species of chydorids. However, there are marked differences in morphology. In *Plurispina chauliodus* and *Planicirclus* the male seta on the antennule is brush-like, whereas all the other taxa have a simple distal segment with no branch setules. *Pleuroxus aduncus* and *Archepleuroxus* have the postabdominal claw of the male sigmoid, whereas the other taxa have the claw much as in the female, except possibly being a little shorter and stouter. In *Pleuroxus hastirostris* there are no postabdominal denticles in the male, just a number of transversely oriented rows or clusters of setae. The shape of the male with reference to that of the females also varies. In many taxa the male is less high relatively than the female, but in *Planicirclus* the males are almost equally round.

*Archepleuroxus* is polyembryonic, and *Archepleuroxus* and *Planicirclus* produce two resting eggs instead of the more traditional one. The amount of pigmentation of the ephippium varies greatly, from being essentially absent in *Pleuroxus foveatus* to such heavy pigmentation in *Plurispina chauliodus* and *Planicirclus* as to obscure all internal details of morphology. Usually the shell flaps that are loosened along the slough line at molting are so broadly connected with the ephippium posteriorly that they almost never are lost completely, but in *Pleuroxus foveatus* the connection is very narrow, and hence the flaps are usually lost, leaving just the shell tooth and seven to ten ventral setae anterior to it still attached to the ephippium.

Thus, there are many differences between these various taxa and even between different populations of what are considered to be the same taxon. This created difficulties in deciding what the limits of the various species are and whether all these species properly belong to the same genus *Pleuroxus*. All the characters, though, have to be considered in cladoceran systematics, as they are part of the diversification that has developed over time.

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## APPENDIX

Table 1. *Pleuroxus* and *Pleuroxus*-like taxa claimed to occur in Australia or New Zealand. *Pleuroxus laevis*, *P. denticulatus*, and *P. similis* described from other continents are probably absent. *Pleuroxus aduncus* from Europe is definitely absent, even though Smirnov & Timms (1983) synonymised *Chydorus denticulatus*, *Chydorus unispinus* and *Alonella nasuta* with it. They also synonymised *Pleuroxus australis* with *P. similis*. *Pleuroxus jugosus* cannot be defined from the single immature female available. The taxa that are numbered are the ones considered in detail in this paper. The paper by Smirnov (1989) describing two species of *Pleuroxus* was published after this paper had been accepted. *Pleuroxus triocellatus* is similar in general style to species 5 to 9 but differs from them in important characters.

| | Taxon | Described from | Comments |
|---|---|---|---|
| 1. | *Pleuroxus aduncus* (Jurine, 1820) | France | Absent from Australia and New Zealand |
| | *Pleuroxus laevis* Sars, 1861 | Norway | Probably absent |
| | *Pleuroxus denticulatus* Birge, 1879 | Wisconsin | Probably absent |
| 2. | *Pleuroxus inermis* Sars, 1896 | New South Wales | Widespread and common in southern Australia |
| | *Pleuroxus similis* Vavra, 1900 | Chile | Probably absent |
| 3. | *Pleuroxus hastirostris* Sars, 1903 | New Zealand | Only in New Zealand |
| | *Alonella nasuta* Smith, 1909 | Tasmania | Seems likely in *Pleuroxus* group but species uncertain. Synonym of *P. aduncus* in Smirnov & Timms (1983) |
| | *Chydorus denticulatus* Henry, 1918 | New South Wales | Synonym of *P. aduncus* in Smirnov & Timms (1983) |
| | *Pleuroxus reticulatus* Henry, 1918 | New South Wales | From type specimen of 1918 and illustrations in Henry (1922), Smirnov (1977) decided this was *Monope reticulata* (Henry, 1922) even though illustrations in Henry (1918) are of a species of *Alonella*. |
| | *Chydorus unispinus* Henry, 1922 | New South Wales | Synonym of *P. aduncus* in Smirnov & Timms (1983) |
| | *Chydorus jugosus* Henry, 1922 | New South Wales | Identity unknown; only immature female available |
| | *Pleuroxus australis* Henry, 1922 | New South Wales | Synonym of *P. similis* in Smirnov & Timms (1983) |
| 4. | *Archepleuroxus baylyi* Smirnov & Timms, 1983 | Western Australia | Known from Victoria, Tasmania and Western Australia |
| | *Pleuroxus triocellatus* Smirnov, 1989 | Western Australia | Apparently different from any species in this table. |
| | *Pleuroxus kakaduensis* Smirnov, 1989 | Northern Territory | Not related to *P. aduncus*. |
| 5. | *Pleuroxus foveatus* n.sp. | Western Australia | |
| 6. | *Plurispina chauliodus* n.gen., n.sp. | Western Australia | |
| 7. | *Plurispina multituberculata* n.sp. | Western Australia | |
| 8. | *Pleuroxus helvenacus* n.sp. | New Zealand | Restricted to New Zealand? |
| 9. | *Planicirclus alticarinatus* n.gen., n.sp. | Western Australia | |

Table 2. Characters of importance in separating the various species and genera.

| Sample no. | Taxon | Region | Sample | Total no. | Length mature females Range (no.) | Surface pattern | Top of shell | Ventral setae Mean | Ventral setae Range (no.) | Ventral setae shell teeth | IP distance (µm) Mean | IP distance (µm) Range (no.) | PP/IP ratio |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1. | *Pleuroxus aduncus* | Denmark | Frey 3004 | 72 | 0.48-0.60(39) | smooth | rounded | 84 | 79-87(19) | 2(0-3), strong | 67 | 63-72(6) | 3.0 |
| 2. | *Pleuroxus inermis* | NSW | Sars F4139 | 199 | 0.44-0.60(190) | smooth | rounded | 88 | 84-93(6) | 1(0-1), very small | 53 | 47-58(3) | 3.8 |
| 2a | | WA | Frey 8026 | 221 | 0.45-0.57(49) | smooth | rounded | 90 | 84-97(19) | 0(0-1) | 53 | 49-58(13) | 4.0 |
| 2b. | | SA | Frey 7961 | 235 | 0.47-0.63(107) | smooth | rounded | 89 | 82-96(15) | 1(0-1) | 59 | 56-63(12) | 3.5 |
| 3. | *Pleuroxus hastirostris* | NZ | Frey 8388 | 235 | 0.40-0.50(61) | smooth | rounded | 78 | 74-81(8) | 1 sharply pointed | 56 | 54-59(6) | 2.6 |
| 4. | *Pleuroxus foveatus* | WA | Shiel 856 | 16 | 0.57-0.65(2) | dimpled | weak ridge | 101 | 93-106(18) | | 46 | 45-47(3) | 6.4 |
| 4a. | | WA | Shiel 857 | 283 | 0.51-0.71(63) | dimpled | weak ridge | 102 | 94-108(17) | 1(0-1) | 47 | 43-50(9) | 6.2 |
| 4b. | | WA | Bayly 51 | 35 | 0.53-0.69(21) | dimpled | weak ridge | 100 | 89-107(12) | | 53 | 52-54(5) | 5.8 |
| 4c. | | WA | Shiel 839 | 107 | 0.49-0.65(67) | dimpled | weak ridge | 102 | 100-113(6) | | 55 | 50-59(7) | 4.7 |
| 5. | *Archeoleuroxus baylyi* | Tas. | Morton 35 | 128 | 0.61-0.95(40) | smooth | rounded | 91 | 84-102(12) | 0(0-1) | 62 | 59-63(3) | 4.7 |
| 6. | *Plurispina chauliodus* | WA | Bayly 31 | 83 | 0.68-0.83(15) | tubercles and ridges | keel | 107 | 100-113(17) | 1, triangular | 42 | 34-47(11) | 7.6 |
| 6a. | | WA | Bayly 58 | 59 | 0.68-0.85(30) | | | | | | | | |
| 6b. | | WA | Bayly 84 | 25 | 0.77-0.90(13) | | | | | | | | |
| 7. | *Plurispina multituberculata* | WA | Bayly 66 | 98 | 0.73-0.88(17) | tubercles and sloping ridges | keel | 122 | 116-127(6) | 1(1-2), triangular | 54 | 52-59(6) | 6.8 |
| 8. | *Pleuroxus helvenacus* | NZ | Frey 8374 | 36 | 0.52-0.89(36) | tubercles and radiating ridges | ridge | 118 | 108-126(19) | 1(0-2) | 56 | 47-61(6) | 5.4 |
| 9. | *Planicirclus alticarinatus* | WA | Shiel 792 | 111 | 1.21-1.75(43) | many ridges | strong keel | 186 | 167-203(20) | 0 | 60 | 47-72(10) | 12.6 |

Table 2 (cont'd). Characters of importance in separating the various species and genera.

| Sample No. | 2nd seta on ODL of TL I brushy? | Gnathobasic filter setae II | III | IV | V | Relative length of regions of postabdomen | Postabdominal denticles | Male seta on antennule brushy? | Male characters | Other characters |
|---|---|---|---|---|---|---|---|---|---|---|
| 1. | no | 8 | 8 | 6 | 4 | preanal=anal<postanal | 7-10, all multiple | no | p.a. tapered; claw sigmoid | |
| 2. | no | 8 | 8 | 6 | 4 | | | | | |
| 2a. | no | 8 | 8 | 6 | 4 | preanal=anal<postanal | 12-13, long | no | | |
| 2b. | no | 8 | 8 | 6 | 4 | | | | | |
| 3. | slightly | 8 | 8 | 6 | 4 | preanal=anal<postanal | 8-10, all multiple | no | no denticles on p.a.; 9 rows of setae | |
| 4. | | 8 | 9 | 6 | 4 | | | | | |
| 4a | no | 8 | 9(8) | 6 | 4 | preanal=anal<postanal | 13-15, long | no | | ephippial shell flaps easily lost |
| 4b | | 8 | 9 | 6 | 4 | | | | | |
| 4c | | 8 | 8(9) | 6 | 4 | | | | | |
| 5 | no | 8 | 8 | 6 | 4 | anal<preanal=postanal | 12 | no | claw short, somewhat sigmoid | 2 ephip. eggs; polyembryonic |
| 6. | | | | | | | | | | |
| 6a. | yes | 10 | 10 | 7 | 5 | preanal<<anal=postanal | 12-15 | yes | 2 strong denticles on rostrum | claw; spines short, setae long |
| 6b. | | | | | | | | | | |
| 7. | no or weakly | 10 | 10 | 7 | 5 | preanal=anal<postanal | 12-15, in different directions | – | | claw; spines short, setae long; tubercles densely packed |
| 8. | no | 8 | 8 | 6 | 4 | preanal<anal<postanal | 20, almost touching at bases distally | – | | p.a. flared outward basally |
| 9. | strongly | 8 | 8 | 6 | 4 | anal<preanal=postanal | 20, very long | yes | tubercle at tip of rostrum | middle and posterior corm setae almost equal; 2 resting eggs; heavy pigmentation in ephip. female |

Table 3. Morphological differences between *Pleuroxus aduncus sensu stricto* from Europe and *Pleuroxus inermis* from Australia.

| Characters | *P. aduncus* | *P. inermis* |
|---|---|---|
| MATURE FEMALE | | |
| Shape | 1. less high | 1. relatively higher |
| | 2. dorsal margin concave near posterior-dorsal angle | 2. dorsal margin evenly rounded, without concavity |
| Shell | 3. 0-4 large denticles at posterior-ventral angle, most commonly 2 | 3. 0-1 very small denticle at posterior-ventral angle, usually 0 in Western Australia population |
| | 4. ventral setae 84 (range 79-89, n=19) | 4. ventral setae 89 (range 82-97, n=40) |
| | 5. submarginal setules along posterior margin short, relatively few, and widely spaced | 5. posterior submarginal setules rather long, numerous, closely spaced |
| Head | 6. IP distance 67 µm (range 63-72, n=5) | 6. IP distance 53-59 µm (range 47-63, n=28) |
| | 7. PP/IP ratio 3.0 | 7. PP/IP ratio 3.5-4.0 |
| Antenna | 8. 1 terminal seta on antennal endopodite much shorter than other 2 | 8. 1 terminal seta on antennal endopodite only slightly shorter than other 2 |
| | 9. no spine on basal segment of exopodite | 9. small spine on basal segment of exopodite |
| Labrum | 10. keel quite broad; tip not strongly attennuated | 10. keel narrower and tip finer |
| Trunklimb I | 11. second spine on ODL extremely small | 11. second spine on ODL longer, quite conspicuous |
| Postabdomen | 12. 7-10 marginal denticle positions | 12. about 12-13 marginal denticle positions |
| | 13. all denticles multiple | 13. distal denticles single; only proximal ones multiple |
| | 14. only a short distal portion of preanal margin not double | 14. longer portion not double |
| | 15. abdominal setae long, reaching middle of anal groove or beyond | 15. abdominal setae shorter, not reaching to one third of anal groove |
| MATURE MALE | | |
| Postabdomen | 16. strongly tapered distally to base of claws | 16. weakly tapered, as in female; not narrowed to base of claws |
| | 17. about 7 oblique rows of spinules (or denticles) in postanal region | 17. about 13 denticles or denticle positions, only a few of proximal ones multiple and weakly oblique, those in distal half nearly all single |
| Postabdominal claws | 18. distinctly sigmoid; longer basal spine irregular | 18. claw and longer basal spine both evenly curved |

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